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A range-wide assessment of carry-over effects within the full annual cycle of the Great Reed Warbler with a focus on sex and population differences

Přenosové efekty v rámci ročního cyklu rákosníků velkých: celoareálová studie se zaměřením na rozdíly mezi pohlavími a populacemi

Diploma thesis

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Prohlášení

Prohlašuji, že jsem závěrečnou práci zpracoval samostatně a že jsem uvedl všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

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Abstract

Movements of long-distance migratory birds are frequently well timed and routed in order to maximise individual fitness. However, individual timing of events or environmental conditions experienced have a potential to carry over into subsequent annual cycle stages and may have delayed fitness consequences. Therefore, knowledge of these seasonal interactions is crucial to identify key periods and regions that limit survival beyond the breeding period and thus to fully understand population dynamics of migratory species. Despite current evidence for seasonal interactions, there is no detailed knowledge of the complex of relationships within the full annual cycle, differences between sexes and populations or impact of environmental conditions during moult in one species.

To unveil this system of seasonal interactions within the annual cycle, we directly tracked 103 great reed warblers (*Acrocephalus arundinaceus*) using light-level geolocators from five breeding sites across the breeding range to obtain information on timing and positions of annual cycle events. We then combined this information with various remotely sensed habitat condition metrics and stable isotopic composition of feathers from the non-breeding grounds to identify and quantify carry-over effects within the full annual cycle.

Our results supported the previously suggested domino effect between timing of consecutive events within migratory phases and buffering capacity of the non-breeding period preventing events to carry over between migratory periods. Contrary to our predictions, we did not identify any strong or moderate effect of habitat quality experienced during the whole non-breeding period but, interestingly, variability of vegetation condition during moult affected both spring migration course and timing of breeding site arrival. Moreover, the carry-over effects appeared to be strongest in the southernmost breeding population compared to central and north European population and did not differ between males and females. Our results provide a first full picture of carry-over effects within the annual cycle in the species and we recommend integrating these results into detailed population models that could better explain species population dynamics.

We also suggest future studies to focus on the effect of inter-specific interaction on the non-breeding grounds on the subsequent annual cycle stages. Finally, as the number of tracking studies is steadily growing, we suggest summarising the current knowledge on seasonal interactions across species and populations in a quantitative review to unveil more general trends.

Keywords: avian migration, light-level geolocators, seasonal interactions, stable isotope analysis, remotely sensed data, timing

Abstrakt

Tažní ptáci překonávají dlouhé vzdálenosti přesně načasovanými a lokalizovanými přesuny s cílem maximalizovat fitness. Načasování jednotlivých fází ročního cyklu a podmínky využívaného prostředí se však mohou přenášet do následujících fází a mohou mít pozdější následky pro fitness jedinců. Znalost těchto sezonních interakcí je proto nezbytná pro lokalizování klíčových období ovlivňujících přežívání jedinců mimo hnízdní období, a tedy pro lepší porozumění populační dynamice tažných druhů. I přes současné vědomosti o sezonních interakcích neexistuje ucelený obrázek o komplexu interakcí v rámci celého ročního cyklu, rozdílech mezi pohlavími a populacemi či vlivu podmínek prostředí v průběhu pelichání u jednoho druhu.

V této studii jsme k odhalení systému těchto sezonních interakcí sledovali 103 rákosníků velkých (*Acrocephalus arundinaceus*) z pěti hnízdních populací napříč hnízdním areálem pomocí světelných geolokátorů. Pro identifikaci a kvantifikaci sezonních interakcí jsme zkombinovali informace o načasování a lokaci jednotlivých ročních fází, rozličné metriky kvality prostředí využívaného na zimovišti získané dálkovým snímáním Země a poměry stabilních izotopů uhlíku v perech vyrostlých na zimovištích.

Naše výsledky analýzy sezonních interakcí ukazují přítomnost dominového efektu načasování událostí tahových období a pufrovací kapacitu zimoviště, která zabraňuje přenosu událostí mezi oběma hlavními obdobími tahu. Oproti očekávání jsme nezaznamenali žádný silný ani střední efekt kvality zimoviště, nicméně vegetační dynamika v období pelichání negativně ovlivňovala délku tahových zastávek v průběhu jarního tahu a načasování příletu na hnízdiště. Přenosové efekty byly častěji nejsilnější u nejjižnější z porovnávaných populací, zatímco u české a švédské populace byly slabší a vzájemně porovnatelné. Mezi pohlavími jsme nezaznamenali žádné rozdíly v síle a směru přenosových efektů. Naše výsledky poskytují komplexní obraz sezonních interakcí v rámci ročního cyklu a doporučujeme začlenění našich poznatků do modelů, které by mohly lépe popsat populační dynamiku druhu.

Budoucí studie by se mohly zaměřit na interakce tažných a stálých druhů na zimovištích a jejich vliv na následující fáze ročního cyklu. Vzhledem k neustále rostoucímu počtu studií sledujících celé roční cykly tažných druhů ptáků navrhujeme data z těchto studií využít ke kvantitativnímu vyhodnocení sezonních interakcí se zaměřením na obecné trendy.

Klíčová slova: analýza stabilních izotopů, dálkově snímaná data, migrace ptáků, načasování, sezonní interakce, světelné geolokátory

Contents

1. Introduction

Billions of birds migrate annually between distinct breeding and non-breeding grounds (Webster et al. 2002, Hahn et al. 2009, Dokter et al. 2018). By undertaking these energetically costly (Wikelski et al. 2003) and often extensive movements (e.g. Egevang et al. 2010, Bairlein et al. 2012), birds track suitable environmental conditions throughout their annual cycles across continents to maximize their fitness (Thorup et al. 2017). Their migratory movements should be thus well routed (Hahn et al. 2019, Jiguet et al. 2019) and precisely timed (Bauer et al. 2016) to match spatiotemporal heterogeneity of the environment.

The choice of a stationary location directly impacts environmental conditions experienced and thus food availability. As migratory flight is energetically demanding (Wikelski et al. 2003), adequate food resources are necessary for the accumulation of fat reserves which directly affect an individual's flight radius (Alerstam and Lindström 1990). Moult is another energetically demanding process (Murphy 1996, Buttemer et al. 2019) and thus lower levels of food resources could prolong moulting period (Murphy and King 1987, Murphy et al. 1988) or impair feather quality (Dawson et al. 2000). Moreover, time spent at the stopover site can increase exposure to predators and thus mortality rate (Middleton et al. 2013) or enhance the risk of being parasitized or infected by pathogens from other animals (Bauer and Hoye 2014). Therefore, stationary site choice has a direct effect on individual's fitness (Alves et al. 2013) that could carry over into the subsequent stages of the annual cycle and has thus a potential to drive species population dynamics (Gill et al. 2001, Norris and Marra 2007).

Environmental conditions vary in time and proper timing of occurrence at the site (Emmenegger et al. 2014) can affect individual fitness through food availability (Kitaysky et al. 1999) or competition (Burgess et al. 2018, Samplonius and Both 2019). The most frequently studied example of differential timing and its consequences for individual fitness is the earlier breeding site arrival in males than in females (Kokko 1999, Morbey and Ydenberg 2001, Briedis et al. 2019). Timing of breeding site arrival may significantly affect the trade-off between forthcoming reproductive success and survival in following years (Nur 1988, Hanssen et al. 2005). Early arriving males tend to occupy high-quality territories which provide them with good chances for higher reproductive success (Smith and Moore 2005, Tarka et al. 2015, Bejarano and Jahn 2018); however, extremely early arrival may reduce their long-term survival probability (Lerche-Jørgensen et al. 2018). Timing of the annual cycle stages is thus crucial for individual fitness (Bauer et al. 2016).

Despite all individuals should maximize their fitness, we often observe a considerable variation in the timing of arrivals and departures as well as reproductive success between

individuals from one population of one species (e.g. Pärt 2001, Liechti et al. 2015, Verhulst et al. 2015). Previous studies showed multiple characteristics of breeding grounds explaining the variation in reproductive success such as weather conditions (Morrison and Bolger 2002), amount of food resources (Murphy 1986, Sillett et al. 2000), nest-site availability (Martin 1995) and predation pressure (Fontaine and Martin 2006). However, Marra et al. (1998) found that habitat conditions experienced at the non-breeding grounds predict timing of the breeding site arrival and thus breeding performance (Norris et al. 2004, Reudink et al. 2009). Their findings suggested that a complex system of mutual relationships between individual states of the annual cycle events – so called carry-over effects – may significantly affect individual fitness and survival of migratory animals (Harrison et al. 2011).

1.1. Carry-over effects

A carry-over effect is defined as a non-lethal dependency between two states (e.g. event timing, individual fitness or habitat condition experienced) of the annual cycle stages with potential delayed fitness consequences (Harrison et al. 2011). These links might affect the timing of subsequent annual cycle events or condition of individuals, resulting in altered reproductive success with a potential to drive population dynamics (Norris and Marra 2007). Information on the presence and strengths of the carry-over effects incorporated into population dynamics models (Norris and Taylor 2006, Ratikainen et al. 2008) have thus a great potential to locate the sources of variability on individual or population levels.

However, the consequences of carry-over effects are not widely known. Norris (2005) suggested either (i) a protagonist mechanism when e.g. loss of habitat causes a reduced population density with a subsequent increase in *per capita* reproduction due to lower density of conspecifics and thus lower levels of competition or (ii) an antagonistic mechanism when e.g. habitat loss will reduce population density as well as body condition of surviving individuals resulting in an overall decrease in *per capita* growth during the reproductive period. The complex system of downstream interactions within the annual cycle gets even more complicated in migratory species. Migratory birds travel annually large distances between breeding and non-breeding areas, visit various stopover locations *en route* and undergo energetically demanding feather moult. Therefore, the number of potential links between different stages of the annual cycle in long-distance migrants increases as well as the difficulty to get information about them.

The most frequently studied link is the impact of non-breeding habitat conditions on the subsequent annual cycle stages. The first proof of this relationship (Marra et al. 1998) showed individuals using mesic habitats during the non-breeding period to be earlier on their non-breeding departure and in better body condition, arriving earlier at their breeding sites and

producing more fledglings (Norris et al. 2004). The following experimental study (Studds and Marra 2005) supported the previous findings and found a proximate cause of the timing differences: mesic habitats yielded more insect biomass and consequently facilitated earlier departure than xeric habitats. This corresponds with a previous finding that food availability at the non-breeding sites limits species abundance (Johnson and Sherry 2001) and can alter body condition during the stationary periods (Strong and Sherry 2000, Latta and Faaborg 2002). Interestingly, studies on between-year survival of long-distance migrants on non-breeding grounds suggested relatively high within-season apparent survival (Sillett and Holmes 2002, Blackburn and Cresswell 2016).

Since the first evidence for the seasonal interactions, numerous studies have been published on this topic. Some indeed found a link between non-breeding habitat conditions and timing of breeding and reproductive success (e.g. Gunnarsson et al. 2005, Goodenough et al. 2017, Saino et al. 2017), some found evidence in some years, for some age- or sex-specific groups of individuals (Rockwell et al. 2012, Drake et al. 2013, López-Calderón et al. 2017, Akresh et al. 2019) or found no support for this association (Drake et al. 2014, McKinnon et al. 2015, Pedersen et al. 2016, Briedis et al. 2018). Similarly mixed is the evidence for the relationship between non-breeding habitat conditions and body condition during migration. Non-breeding habitat was shown to affect individual condition *en route* (Bearhop et al. 2004), or stopover arrival timing but not individual condition (Paxton and Moore 2015). A multi-species study (González-Prieto and Hobson 2013) looking at links between non-breeding habitat conditions and body condition or timing of arrival found evidence for carry-over effects in two out of seven species on one trait but there were no carry-over effects detected in other species.

Direct tracking of migratory individuals has brought valuable information about full annual cycles by revealing timing of all major annual cycle events and the location of sites visited. It is thus not surprising that researchers have taken this advantage to better understand carry-over effects within the full annual cycle. Recent studies found a domino effect of consecutive event timing where the strongest time dependencies occur during the post- and pre-breeding periods (Briedis et al. 2018, Gow et al. 2019), within the post-breeding period only (Senner et al. 2014) or mainly between the breeding site arrival and onset of breeding and the end of breeding and breeding site departure (van Wijk et al. 2017). Interestingly, all these studies concluded that the non-breeding period buffers against the accumulation of carry-over effects within the annual cycle (Senner et al. 2014, van Wijk et al. 2017, Briedis et al. 2018, Gow et al. 2019). Briedis et al. (2018) investigated also the impact of non-breeding habitat conditions and did not find an effect either on the timing of breeding site arrival or on the start of breeding. This finding corresponds to the

result of McKinnon et al. (2015) who found a link between non-breeding habitat conditions and the non-breeding ground departure only but no carry-over effects to the subsequent phases of the pre-breeding period.

1.1.1. Sex differences in carry-over effects

Differences in migratory behaviour between males and females may result in their spatial segregation on non-breeding grounds (Marra and Holmes 2001, Catry et al. 2004, de Zwaan et al. 2019) or sex differences in timing of the annual cycle events (Briedis et al. 2019). Large- or fine-scale spatial segregation could have multiple consequences for individuals such as differences in flight distances to breeding grounds, experiencing different habitat types of various quality or dissimilarities in non-breeding habitat dynamic over time with subsequent density-dependent compensation effects during the reproduction period (Gill et al. 2001, Briedis and Bauer 2018). Similarly, the differences in timing of the annual cycle between the sexes can lead to exposure to harsh conditions *en route* with following survival costs of the early arriving sex (Lerche-Jørgensen et al. 2018). Moreover, females are slightly smaller than males in the majority of passerine species (e.g. Lehikoinen et al. 2017, Briedis et al. 2019) and these body size differences could also affect multiple aspects such as fat loads and thus flight radius (Alerstam and Lindström 1990, Alerstam 1991). Despite an extensive knowledge about the inter-seasonal or year-round links between particular stages of the annual cycle (especially their timing), there is only little information about sex-differences in carry-over effects and its potential consequences for individual fitness.

Despite the clear differences in timing of migration between sexes (Briedis et al. 2019), the differences in carry-over effects seem to be inconsistent. Some studies suggested that females have more interactions between individual annual cycle events than males (Drake et al. 2013), some studies suggested the opposite (Rushing et al. 2016, López-Calderón et al. 2017) and some found no sex differences in carry-over effects but a likely fine-scale habitat segregation on non-breeding grounds (Akresh et al. 2019). So far, only one study tested sex-specific carry-over effects within the full annual cycle using barn swallows (*Hirundo rustica*; Saino et al. 2017). They showed females to be more sensitive than males to delayed timing of annual cycle events and harsher habitat conditions experienced at the non-breeding sites resulting in delayed spring arrival and lower reproductive success in females (Saino et al. 2017). However, nothing is known about sex-specific fine-scale connectivity contributing into sex-segregation into different habitats. Some females could occupy drier habitats (Marra and Holmes 2001), might leave non-breeding grounds later than males (Studds and Marra 2005) with negative consequences for the upcoming reproduction period (Norris et al. 2004).

1.1.2. Breeding latitude impacts on carry-over effects

Breeding latitude affects timing of events throughout the annual cycle with individuals from higher breeding latitudes delaying all annual cycle events compared to those from lower latitudes (Conklin et al. 2010, Briedis et al. 2016, Jahn et al. 2019). These differences might cause a leap-frog migration (Alerstam and Högstedt 1980, Bell 1996) where higher-latitude populations spend the boreal winter further of the lower-latitude breeding populations. This pattern leads to differential migration of populations experiencing different non-breeding habitats and stopover conditions at different times with potentially delayed fitness consequences (Briedis and Bauer 2018). This is enforced by the evidence that the optimal arrival window width decreases with increasing latitude (Hahn et al. 2016) where a little temporal mismatch could strongly impact an individual's fitness. Contrary to these findings, arrival timing in yellow warblers (*Setophaga petechia*) breeding north of the Arctic Circle was not affected by the local conditions experienced during the non-breeding period (Drake et al. 2014). On the other hand, yearling females of yellow warblers breeding in lower latitudes were found to delay their breeding arrival and have lower reproductive performance when experiencing xeric habitats on their non-breeding grounds in Central America (Drake et al. 2013). So far, the most complex study on breeding-latitude impacts on the timing of the annual cycle events was conducted on the aerial tree swallow (*Tachycineta bicolor*; Gow et al. 2019). Gow et al. (2019) deployed light-level geolocators to directly track tree swallows from 12 North American breeding sites to unveil the main dependencies between the timing of the annual cycle events. Breeding latitude affected the timing of breeding, breeding site departure, post-breeding migration and non-breeding ground arrival. However, the effect of breeding latitude disappeared during the non-breeding period and the timing of departure from the non-breeding grounds was independent of the breeding destination (Gow et al. 2019).

1.2. Feather moult

Complete feather moult typically occurs in small bird species every year and keratin synthesis during moult was found to be energetically demanding (Murphy 1996, Portugal et al. 2018, Buttemer et al. 2019). Passerine birds have multiple strategies where and when to replace certain types of feathers (Pyle et al. 1987, Jenni and Winkler 2010). Complete moult on the non-breeding grounds is a common strategy among many long-distance migratory birds breeding in the Western Palearctic (Kiat et al. 2019) as this strategy could be advantageous due to a spatiotemporal separation of the energetically demanding periods such as breeding, migrating and moulting (Kiat et al. 2019).

Late timing of moult negatively affects fuel accumulation and preparation for spring migration (Merilä 1997, Rubolini et al. 2002) with a potential to reduce the ability to accumulate fat with negative implications for migration speed (Lindström et al. 2019). Moreover, late moult can result in increased moult speed but in decreased quality of feathers (Dawson et al. 2000) with potential adverse implications for flight performance and flight energetics (Tomotani et al. 2018). For instance, Stutchbury et al. (2010) showed that late-breeding wood thrushes (*Hylocichla mustelina*) delayed the start of post-breeding moult reducing body condition and postponing breeding site departure. Interestingly, the delayed timing and reduced body condition did not carry over to the non-breeding ground arrival.

Although conditions outside the breeding grounds are probably of great importance, there is only a limited number of studies on carry-over effects within the full annual cycles. Moreover, there is only rudimentary knowledge about both the time dependencies of the annual cycle events and the impact of habitat conditions experienced by individual birds. This lack of knowledge is caused by an incredibly challenging task to track full annual cycles in small bird species resulting in widely missing information about the complex of downstream relationships within the full annual cycle (Marra et al. 2015).

1.3. Advances in tracking technologies

The recent miniaturization of light-level geolocators and its application in movement ecology of small bird species has enabled researchers to unveil crucial spatiotemporal information on full annual cycles of many small bird species (Stutchbury et al. 2009, McKinnon and Love 2018) with reasonable sample sizes (e.g. Stanley et al. 2015). These tiny devices (weighing from 0.3 g) measure light intensity over time that can be further used to estimate positions based on a simple principle of solar navigation (Hill 1994). After retrieving these archival tags and downloading the data, longitude is estimated from the time of local noon/midnight and latitude from the day-/night-lengths, providing two position estimates per 24-hour period (Lisovski and Hahn 2012). Massive deployment of these tags to small migratory bird species has yielded extensive data for testing hypotheses on strategies of crossing major topographical barriers (Adamík et al. 2016), intra-tropical movements within non-breeding grounds (Heckscher et al. 2015, Koleček et al. 2018), non-breeding spread of individuals from the same breeding population (Finch et al. 2017) or enabled to locate moulting regions (Grissot et al. 2019). Similarly, the recent miniaturization of archival GPS tags has enabled researchers to assess, for the first time, stationarity of individuals at their non-breeding sites (Pedersen et al. 2019), fine-scale migratory connectivity (Fraser et al. 2017) and habitat use (Hallworth and Marra 2015) in small bird species.

1.4. Habitat condition assessments

Migratory birds spend a significant part of their annual cycle at non-breeding grounds (e.g. Schmaljohann et al. 2012, Briedis et al. 2016) and the non-breeding habitat conditions have been shown to impact subsequent phases of the annual cycle such as body condition during migration (Bearhop et al. 2004), timing of breeding site arrival and reproductive success (Norris et al. 2004). Non-breeding sites of individuals from one breeding population can cover wide areas (Koleček et al. 2016, van Wijk et al. 2018) often in tropical and subtropical regions (Newton 2008) which are usually hardly accessible causing a research bias towards the temperate zone (Titley et al. 2017). All this makes the research of migratory behaviour, body condition and habitat use beyond the breeding grounds extremely challenging.

Recently, numerous satellites have been released to orbit the Earth in order to collect various data about biosphere, atmosphere as well as land and water surfaces (Jensen 2000). Despite various metrics currently available, the Normalized Difference Vegetation Index (NDVI) is the most frequently used remotely sensed variable in the field of ecology (Pettorelli 2013). The index is calculated from data sensed by two simple sensors measuring the amount of near-infrared (NIR) and red (R) light reflected from the surface. These sensors are thus available on many satellites providing sufficient spatial and temporal coverage (Gillespie et al. 2008). The following equation is used for NDVI calculation (Pettorelli 2013):

$$NDVI = \frac{(\mathrm{NIR} - \mathrm{R})}{(\mathrm{NIR} + \mathrm{R})}$$

Plant chlorophyll strongly absorbs the visible light (wavelength of 400–700 nm) which is further used for organic molecule synthesis while mesophyll cells reflect the near-infrared light (wavelength of 700–900 nm) to prevent overheating of plant tissues which causes a decrease in photosynthesis efficiency (e.g. Bazzaz 1979). Therefore, the amount of chlorophyll in the leaves and the number of leaves positively correlate with red light absorbed and thus with NDVI values (Tucker and Sellers 1986, Sellers 1987). Dense and healthy vegetation shows the highest integrated NDVI values around 0.5–0.7 depending on vegetation type, sparse shrub has values around 0.4 and bare soil, rocks and water the lowest values ranging from 0–0.15 (Pettorelli 2013).

The utility of NDVI values for ecological research is supported by a positive correlation of NDVI and the amount of precipitation on both continental (Tucker and Newcomb 1991) and local scales (Schmidt and Karnieli 2002). The amount of precipitation is a good measure of primary net productivity of the environment which is linked to species richness (Nagendra 2001) as well as to the abundance of invertebrates on small scales (Hahn et al. under review). NDVI values integrated over time and areas summarize vegetation structure and health over time and can be used as

a primary net productivity measure within a certain period of time (Pettorelli et al. 2005, Pettorelli 2013) reflecting local conditions experienced by the animals living in the region (Saino et al. 2004a, b). Changes in NDVI values over time reflect leaf development or degradation processes and could be used for the calculation of green-up or senescence timing (Pettorelli et al. 2007) and for studying the consequences of local breeding habitat conditions for migratory birds (Emmenegger et al. 2016).

Another indirect approach to assess habitat conditions is the analysis of stable isotope composition. Stable isotopes are widely used in biology (Lajtha and Michener 1994) and movement ecology (Hobson 1999). During tissue formation, elements (most frequently H, C, N, O and S) are incorporated in a specific ratio between a common isotope (e.g. ^{12}C) and its heavier isotope (not radioactive, e.g. ^{13}C). The ratio between the heavier and the common isotope (e.g. $^{13}C/^{12}C$) can be used as a geographic, dietary or habitat marker (Marra et al. 1998, Bearhop et al. 2005, Sorensen et al. 2009). Some animal tissues are metabolically inert once grown (such as bones or feather and claw keratin) and the stable isotopic composition from the tissue formation is permanent; on the contrary, some tissues are continuously changing together with its stable isotopic signal (such as blood, muscles or livers; Hobson and Clark 1993, Lourenço et al. 2015). Stable carbon isotopes ($^{13}C/^{12}C$) are frequently used as a marker of vegetation structure (Marra et al. 1998, Drake et al. 2013, González-Prieto and Hobson 2013, Akresh et al. 2019) as this isotopic ratio was shown to reflect habitat characteristics on the mesic–xeric gradient (Bearhop et al. 2004, Studds and Marra 2005). These differences between habitat types arise from differential assimilation of atmospheric molecules of carbon dioxide in C_3, C_4 and crassulacean acid metabolism (CAM) photosynthetic pathways. C_3 plants (such as trees, shrubs and other dicotyledonous plants) prefer cooler and more moist conditions (values more depleted in ^{13}C) whereas C_4 and CAM plants (typically grasses and succulents) prefer drier and warmer conditions (values more enriched in ^{13}C; Pearcy and Ehleringer 1984, Yamori et al. 2014). The ratio of these plant types at a given site thus reflects the water availability in the habitat (O'Leary 1981, Farquhar et al. 1989) or could be used to estimate the geographic origin of the tissue (Still et al. 2003).

1.5. Study species

The great reed warbler (*Acrocephalus arundinaceus*) is a 30-g insectivorous passerine breeding in reedbeds of the Western and Central Palearctic (Cramp 1992, BirdLife International 2019). Direct tracking of individuals breeding in Europe and the Middle East revealed population-specific non-breeding regions in sub-Saharan Africa (Lemke et al. 2013, Horns et al. 2016, Koleček et al. 2016). Moreover, observational studies from sub-Saharan non-breeding grounds suggest that great reed warblers prefer wetter habitats, dense vegetation or reedbed-like habitats to dry savannahs

(Becquaert 1952, Ruwet 1965, De Roo and Deheegher 1969, Sorensen et al. 2015). On average, tracking data showed that European breeding birds leave their breeding sites during late August and arrive at the non-breeding grounds during early September. Subsequently, the non-breeding ground departure occurs around mid-April and arrival at their breeding grounds around early-May (Koleček et al. 2016).

The tracking data unveiled a wide spatial spread of individuals from one breeding population on non-breeding grounds (weak migratory connectivity; Webster et al. 2002, Koleček et al. 2016). Moreover, distant intra-tropical movements between two or three non-breeding sites were detected during the non-breeding period in the majority of tracked individuals (Koleček et al. 2016). These intra-tropical movements from northern sites towards southern sites in late November are likely an adaptation for the dramatic changes in the sub-Saharan habitats (Koleček et al. 2018) linked to the seasonal variation in precipitation and vegetation development and degradation in the Sahel region (Sultan and Janicot 2003). Timing of these movements is probably linked also to the completion of moult that starts shortly after the arrival at the non-breeding grounds in northern sub-Saharan Africa (Pearson 1975, Hedenström et al. 1985, Bensch et al. 1991, Sorensen et al. 2016). The duration of the complete moult in the great reed warbler was estimated to 77.5±24.1 days (mean ± SD; n = 4; according to Hanmer 1979, Bensch et al. 1991) that corresponds to the average duration of complete moult in long-distance migrants (Ginn 1983, Kiat et al. 2019). Observations of freshly moulted individuals in southern parts of the species' non-breeding range suggest that moult is completed before the intra-tropical movement in populations wintering in the northern parts of the non-breeding range (De Roo and Deheegher 1969, Pearson 1975, Hanmer 1979, Hedenström et al. 1985, Sorensen et al. 2016).

Great reed warblers are facultatively polygynous and each female usually raises one brood per year (Cramp 1992). The long-term research on the Swedish breeding grounds showed that life-time number of fledglings and recruits is directly linked to the timing of spring arrival; individuals with advanced spring arrival produced more fledglings and recruits compared to individuals with delayed spring arrival (Tarka et al. 2015). Moreover, early arriving males have a higher probability to become polygynous and thus raise more offspring (Hasselquist 1998) suggesting a direct link between the annual cycle timing, individual fitness and population dynamics in this species. These finding concur with the theory stating that early spring arrival facilitates occupancy of high-quality territories providing more food for offspring and thus increasing fitness of such an individual (Morbey and Ydenberg 2001, Kokko et al. 2006).

1.6. Study aims

To improve the knowledge of time dependencies within the annual cycle and impacts of non-breeding habitat conditions on subsequent annual cycle events, we use a robust dataset of full annual tracking of great reed warblers from five breeding populations. Moreover, we focus on the differences in these carry-over effects between males and females and between individuals from latitudinally-distinct breeding populations. Similarly, we evaluate the impacts of dissimilarities between moulting period and the whole non-breeding period habitat conditions on the subsequent phases of the annual cycle. To detect these carry-over effects and estimate the strength of these relationships within the annual cycle, we combine spatiotemporal information derived from light-level geolocators, spatiotemporally- and individually-specific remotely sensed data combined with stable isotopic signatures from tissues grown on the non-breeding grounds.

2. Predictions

1. We predict a domino effect between consecutive events: advanced timing or faster migration will cause an advance in timing of consecutive annual cycle phases (Piersma 1987, Gow et al. 2019).
2. The non-breeding period will act as a buffer zone preventing the post-breeding migration timing to carry over into the pre-breeding period (Senner et al. 2014, Briedis et al. 2018, Gow et al. 2019).
3. Harsh non-breeding habitat conditions will negatively affect the timing of non-breeding ground departure, slow down spring migration course and delay timing of breeding site arrival (Marra et al. 1998, Bearhop et al. 2004, Norris et al. 2004).
4. Due to equivocal evidence for sex differences in carry-over effects, we only predict stronger carry-over effects within the pre-breeding period in males than in females due to a higher probability of encountering suboptimal conditions *en route* with its detrimental consequences (Briedis et al. 2017).
5. There is only little knowledge about potential differences in carry-over effects between individuals from distinct breeding latitudes. However, we predict that carry-over effects will occur more frequently and will be stronger in individuals breeding at higher latitudes, especially, during the pre-breeding period. These differences might arise from a shorter arrival window due to a shorter green-up period (Hahn et al. 2016) and a higher probability of encountering a cold spell with its negative impacts on the timing of migration (Briedis et al. 2017).
6. Lower-quality habitats experienced during moult will have a stronger negative effect on the subsequent annual cycle events than the habitat conditions experienced during the entire non-breeding period as moult is a highly energetically demanding process (Murphy 1996, Portugal et al. 2018, Buttemer et al. 2019).

3. Material and methods

3.1. Data collection

We used information on 103 full annual cycles (all stages between breeding site departure and arrival in the following year) obtained from light-level geolocators retrieved from adult great reed warblers (38 females, 64 males and 1 of unknown sex) breeding in five populations in Sweden (SE; 59°N, 15°E), Czech Republic (CZ; 49°N, 17°E), Bulgaria (BG; 44°N, 26°E), Turkey (TR; 42°N, 36°E), and Kazakhstan (KZ; 47°N, 62°E) from 2010 to 2018 (fig 1). In 10 individuals from SE and CZ in which the breeding site arrival was not available from the light-level recording, we used the date of first re-encounter of colour-ringed individual at the breeding site as the geolocator-derived and observed breeding site arrivals highly correlated in individuals with both measures (Pearson's correlation test: $\rho = 0.99$, $df = 25$, $P < 0.001$). For details on the sex-specific number of recaptured individuals in each year and population and geolocator specification see Appendix 1. From 52 recaptured individuals, we collected either the distal part of a fifth primary (BG, n = 12), a third tail feather (SE, n = 17 and TR, n = 4), or a second tertial (CZ, n = 19) during geolocator retrieval for further stable isotopic analyses.

3.2. Geolocator analysis

We estimated sunrises and sunsets from the log-transformed light-level recordings using *preprocessLight* function from twGeos package (Wotherspoon et al. 2016). For further analysis, we used functions from GeoLight package version 2.0.0 (Lisovski and Hahn 2012). We applied a *loessFilter* function (k = 2) to exclude unlikely timed sunrises and sunsets and *changeLight* function (quantile = 0.9; days = 2) to distinguish stationary and non-stationary periods. To calculate geographic positions of the stationary locations during the whole annual cycle, we used in-habitat calibration estimating the corresponding sun elevation angle (SEA) using the period when the bird occurred at a known breeding location. We then merged consecutive stationary periods with ~50% overlap in longitude as *changeLight* function frequently splits long stationary periods into short ones. We also visually checked the geographic span of all sites where the individual spent less than a week and considered the ones with span over ~300 km as nonstationary. We used the Hill-Ekstrom calibration when the positions using in-habitat calibration SEA resulted in unreliable positions (e.g. in the sea or desert; n = 11), to find out SEA with a minimum variation of the geographic positions. Subsequently, we used the SEA to calculate positions of all stationary sites for each individual. We calculated the geographic position for each stationary period as the modus of the geographic coordinates and considered all stationary locations south of 20°N and lasting

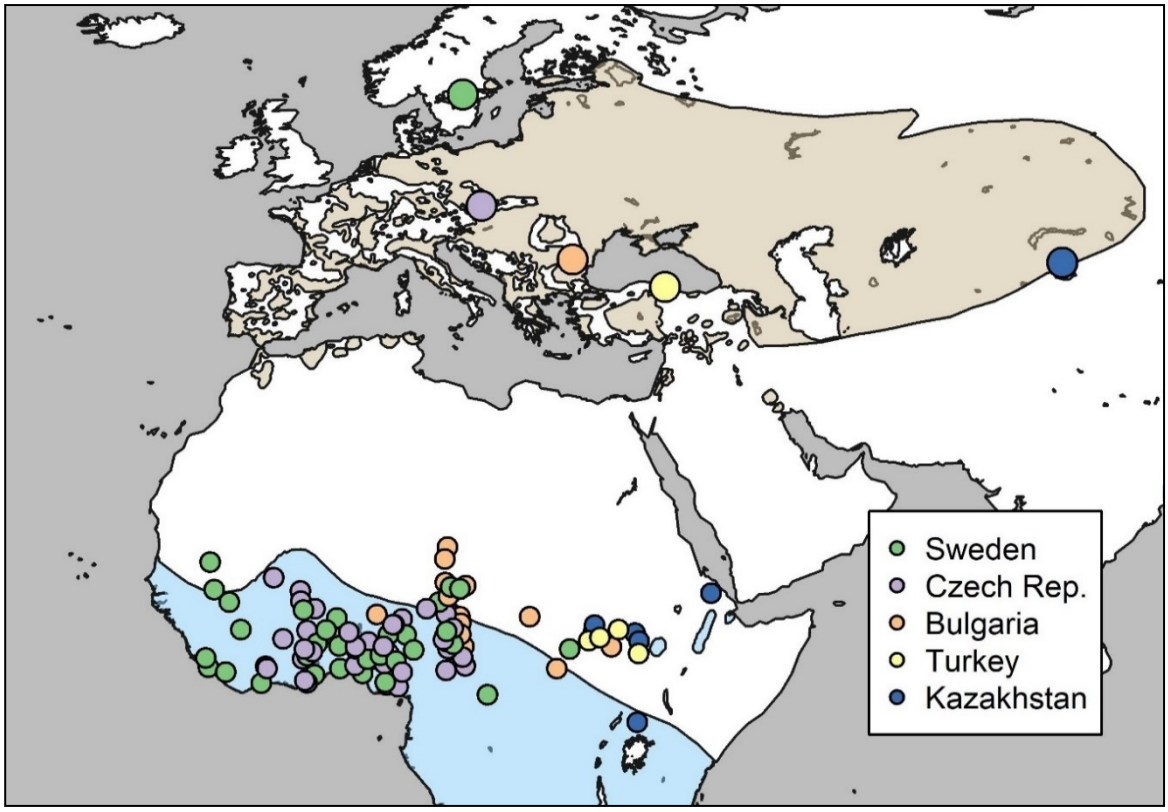

Figure 1: Map presenting the breeding (beige) and non-breeding range (blue) of the great reed warbler (BirdLife International 2019). Large points depict study sites and small points represent the first non-breeding sites of all individuals included in the analysis (n = 103).

more than 23.5 days (longer than 90% of all stationary locations north of 20°N) as non-breeding sites (fig 1). Other stationary locations were considered stopovers or breeding sites.

3.3. Stable isotope analysis

We used stable isotope ratios from 52 feather samples grown in sub-Saharan Africa during tracking to determine the habitat used during the moult period. Prior to stable isotope analysis, feathers were washed in 2:1 chloroform:methanol solution, then rinsed with distilled water and left to air dry for 24 h. Feather keratin samples of about 300 µg, pre-weighed in tin cups, were combusted using the vario Micro cube elemental analyser (Elementar, Analysensysteme, Germany) and the resultant CO_2 gases were introduced into a Micromass Isoprime isotope ratio mass spectrometer (Isoprime, Cheadle Hulme, UK) via a continuous flow-through inlet system. Sample $^{13}C/^{12}C$ ratio is expressed in the conventional delta notation ($\delta^{13}C$) in per mil (‰) and the values are relative to the Vienna Pee Dee Belemnite standard. We obtained stable isotope ratios by using the equation:

$$\delta^{13}\mathrm{C}\ (‰) = 1000 \times \left(\frac{^{13}\mathrm{C}_{sample}/^{12}\mathrm{C}_{sample}}{^{13}\mathrm{C}_{standard}/^{12}\mathrm{C}_{standard}} - 1\right).$$

Repeated measures of internal laboratory standards indicate that our measurement error (SD) was ± 0.05%. Stable isotope analysis was conducted in the Stable Isotope Laboratory at the Institute of Limnology, University of Konstanz, Germany by Dr Elizabeth Yohannes.

3.4. Habitat characteristics

We employed two techniques to describe non-breeding habitat conditions – assembling remotely sensed Normalized Difference Vegetation Index (NDVI) values and stable isotope analysis. We used NDVI to calculate integrated greenness, vegetation dynamics and greenness trend used by each individual during its presence at the known non-breeding sites. NDVI values are provided by the North Oceanic and Atmospheric Administration as weekly data at 4-km resolution (acquired from ftp://ftp.star.nesdis.noaa.gov/pub/corp/scsb/wguo/data/Blended_VH_4km). Due to the low accuracy of the positions estimated from light-level recordings (Fudickar et al. 2012, Lisovski et al. 2012), we considered an area of 44×44 km around each non-breeding location as an area of potential occurrence over the period when each individual was present at the non-breeding site (fig 2; for more details see *Sensitivity analysis*). As previous observational studies suggested great reed warblers to prefer microhabitats with higher water availability at their non-breeding grounds (Becquaert 1952, Ruwet 1965, De Roo and Deheegher 1969), we gathered weekly 3rd quartiles of NDVI values from the area of potential occurrence to avoid dry habitats in the area of potential occurrence (for pairwise comparison of different weekly metrics see Appendix 2 and *Sensitivity analysis*).

We then calculated the following characteristics for each individual on a corresponding spatiotemporal scale: (i) integrated greenness as the average of weekly 3rd quartile values, (ii) vegetation dynamics as the average of absolute between-week differences and (iii) greenness trend as the sum of between-week differences over time (fig 2). For individuals with more than

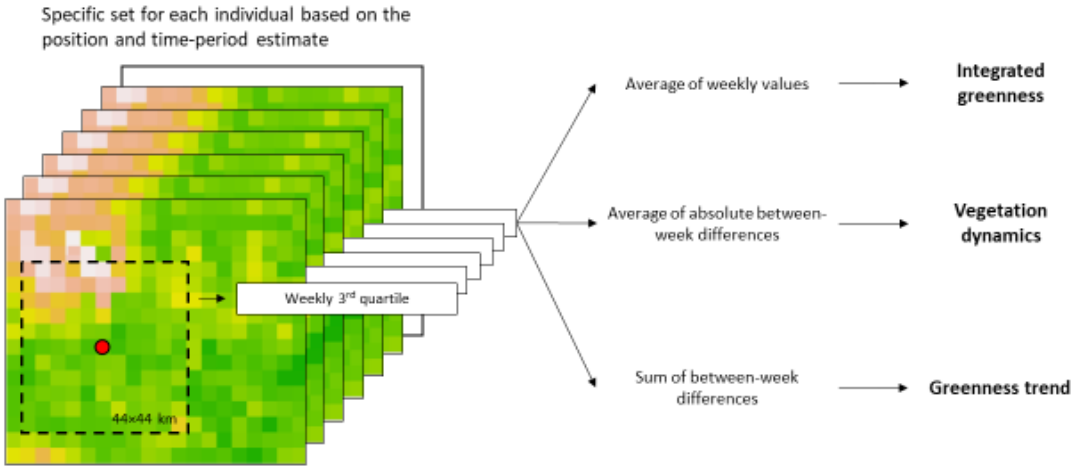

Figure 2: Schematic sketch of the NDVI calculation for assessing habitat characteristics.

one non-breeding site, we calculated non-breeding habitat characteristics as a weighted average of values from each site with a number of weeks spent at the site as a weight. Moreover, to characterise the state of habitat on the mesic–xeric gradient we used $\delta^{13}C$ values indicating the ratio of C_3/C_4 plants and thus water availability in the habitat during the feather synthesis (moult period).

To test our assumption of higher NDVI values in the habitats with higher water availability with likely higher probability of occurrence of tracked birds, we calculated integrated greenness and intra-annual variation of NDVI values in four main African wetlands (Inner Niger Delta, Chad Lake, Sudd swamps and Okavango Delta) and their surroundings. We gathered weekly values with a 4-km pixel resolution for three points inside and three points outside each wetland in the year 2013 (fig 3) and calculated integrated greenness and vegetation dynamics as described above. To compare primary productivity and its intra-annual variation at wet and dry sites, we fitted two linear mixed effect models adopting *lmer* function from lme4 R package (Bates et al. 2015) with location of point inside/outside wetland as a fixed effect and wetland identity as a random intercept. Wetland habitats showed on average higher values of integrated greenness values than habitats outside the wetlands (estimate = 0.33; SE = 0.024; $P < 0.001$) while the vegetation dynamics during the year was higher at points outside the wetlands than at points inside the wetland (estimate = 0.01; SE = 0.001; P = 0.001; fig 3).

3.5. Partial least square path models

We employed partial least square path models (hereafter 'path models'; Henseler et al. 2012a, Henseler et al. 2012b, Dijkstra and Henseler 2015) adopting plspm R package functions (Sanchez 2013, Sanchez et al. 2017) to detect and quantify carry-over effects between individual stages of the annual cycle. Path models enable to simultaneously fit a set of multiple regressions (Hair et al. 2017) where a variable can be explanatory (exogenous), or both explanatory and response (endogenous) with only a limited number of distributional assumptions (Cassel et al. 1999). We used manifest variables (table 1) expressing the states of the annual cycle events such as timing of events, migration course and environmental characteristics. These variables were then used for developing a full initial path diagram based on proposed predictions 1–3 (see *Predictions*; fig 4). We then prepared a set of reduced initial path models using the previous initial path model but additionally testing predictions 4–6 and thus using data differing in sample sizes.

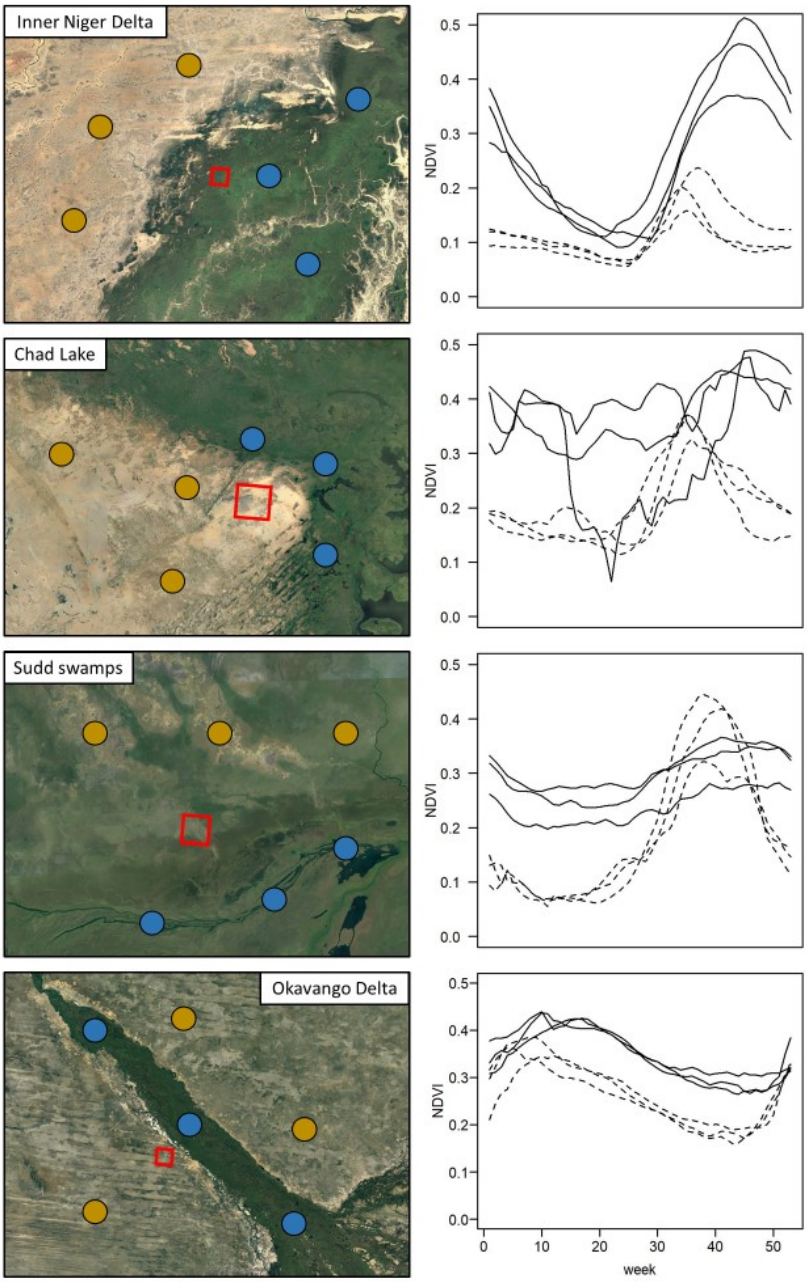

Figure 3: Four main African wetlands and the position of points used for collecting NDVI data. Blue points reflect wet sites inside the wetland and beige points reflect dry sites outside the wetland (Google Maps 2019). Red squares indicate the NDVI pixel size of 4×4 km (left panels). Solid lines connect weekly values of NDVI inside the wetland and dashed lines NDVI values at points outside the wetland. Dates are expressed as week numbers of the year 2013 (right panels).

Therefore, we reduced the number of relationships within these initial path models to test all predictions following the rule of minimum of 10 observations per explanatory variable (Cohen 1992, Barclay et al. 1995; Appendix 3). In total, we prepared four sets of path models examining (1) relationships within all stages of the annual cycle (path model 1; predictions 1–3; n = 103 individuals; fig 4), (2) differences in carry-over effects between sexes (set of path models 2;

Table 1: Variables used to describe states of the annual cycle events, abbreviations used in figures and their descriptions.

Variable	*Abbreviation*	*Description*
Breed site departure	Depart breed	Date of departure from the breeding site
Autumn migration strategy	Autumn migration	Ratio of the duration of stationary locations during autumn migration to the duration of autumn migration
Non-breeding ground arrival	Arrival non-breed	Date of arrival at the first non-breeding site
$\delta^{13}C$	$\delta^{13}C$	Ratio of stable carbon isotopes in feathers grown on the non-breeding grounds
Integrated greenness	Greenness	Integrated greenness at all non-breeding sites visited
Greenness trend	Greenness trend	Trend of the greenness values over time at all non-breeding sites visited
Vegetation dynamics	Veg. dynamics	Variability of the greenness values over time at all non-breeding sites visited
Non-breeding ground departure	Depart non-breed	Date of departure from the last non-breeding site
Spring migration strategy	Spring migration	Ratio of the duration of stationary locations during spring migration to the duration of spring migration
Breeding site arrival	Arrival breed	Date of arrival at the breeding site

predictions 1–4, one path model for each sex; females = 38, males = 54), (3) differences in carry-over effects between individuals from breeding sites with different latitude (set of path models 3; predictions 1–3 and 5; one model for each country with sufficient sample size: SE = 37, CZ = 35 and BG = 21) and (4) differences in carry-over effects of the habitat conditions during the moult period and whole non-breeding period on the subsequent annual cycle events (set of path models 4; predictions 1–3 and 6; one model for each period; n = 52; see Appendix 3 for all reduced initial path models). In the set of path models 2, we used data from SE, CZ and BG where both sexes were studied. Similarly, we included only individuals with at least two non-breeding sites where we could estimate the duration of the first non-breeding period in the set of path models 4. We refer to path coefficients over 0.5 as strong effects, 0.3–0.5 as moderate effects and coefficients below 0.3 as weak effects (Cohen 1977).

As random term specification is not implemented in the path models, we scaled and centred all variables within a population prior to fitting path model 1, and set of path models 2

and 4. Moreover, we fitted a set of linear mixed effect models (using *lmer* function) with year as a fixed factor effect and population as a random intercept to explore between-year differences in each variable. For each of these models, we calculated marginal and conditional R^2 (Nakagawa and Schielzeth 2013) using *r.squaredGLMM* function from MuMIn R package (Barton 2018). As we found little or no inter-annual differences, we do not consider year as an important source of variability in the variables (see Appendix 4). Finally, we employed the *plspm* function from the plspm R package (Sanchez et al. 2017) to fit all path models and bootstrapped the resulting path model with 1×10^4 iterations to obtain 95% confidence intervals for each path coefficient. Prior to fitting path models testing differences between moulting and whole non-breeding period, we assessed collinearity of $\delta^{13}C$ and integrated greenness from the first non-breeding site (for individuals with at least two non-breeding sites) to determine whether the variables should be considered manifest variables of one latent variable or independent manifest variables. We present the direct and indirect path coefficients between variables and R^2 as a measure of the variation explained in each endogenous variable in the path model. We consider path coefficients statistically important when confidence intervals do not overlap zero and different from each other when confidence intervals do not overlap each other.

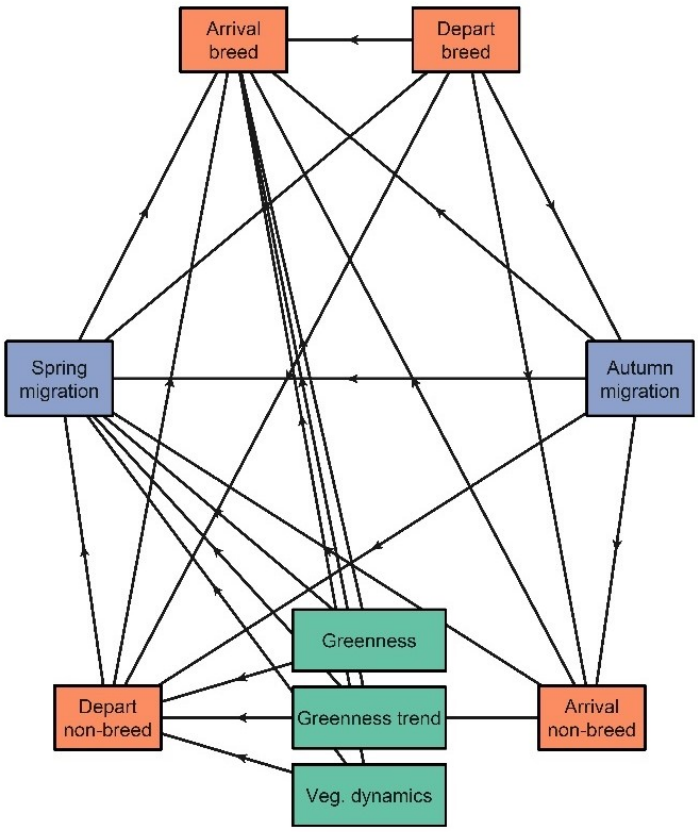

Figure 4: Full initial path model testing predictions of carry-over effects (see *Predictions*) within the full annual cycle.

3.6. Sensitivity analysis

Due to the imprecision of latitude estimates from light-level recordings (Fudickar et al. 2012, Lisovski et al. 2012), we collected NDVI values (integrated greenness, greenness trend and vegetation dynamics) from two additional areas of potential occurrence (latitude×longitude; 144×44 km and 244×44 km) besides the 44×44 km described above and calculated three path models employing the reduced path model structure from Appendix 3D using environmental characteristics with different resolutions (Appendix 5A). Since the results did not differ, we exercise the most precise data from the 44×44 km area of potential occurrence around position estimates. We decided to use this spatial resolution as data derived from bigger areas of potential occurrence could bias individual estimates of habitat conditions because NDVI is highly latitudinally stratified and variable within the sub-Saharan region where the majority of tracked individuals spent the boreal winter (Pettorelli 2013, Zhou et al. 2016).

Similarly, we tested the effect of our assumption for the use of higher quality habitats with higher NDVI values (fig 3) using three additional weekly measures of NDVI within the area of potential occurrence. Beside the weekly 3rd quartile values (fig 2), we calculated also mean, median and maximum values within the area of potential occurrence and calculated the same habitat condition metrics as presented above. Then, we fitted four path models (for each type of weekly measure one) employing a reduced path model scheme presented in Appendix 3D. As we obtained similar results using all metrics (Appendix 5B), we decided to use habitat condition metrics calculated with weekly 3rd quartiles as findings in literature suggest great reed warblers to prefer wet non-breeding habitats (Becquaert 1952, Ruwet 1965, De Roo and Deheegher 1969), and we found higher integrated greenness values in major African wetlands (fig 3). We used R version 3.5.3 for all calculations and analyses (R Core Team 2019).

4. Results

We found the strongest carry-over effects between timing of the breeding site departure and non-breeding ground arrival (path coefficient = 0.60; 95% confidence interval: [0.46; 0.74]) and non-breeding ground departure and breeding site arrival (0.78; [0.64; 0.91]). Moreover, individuals with longer stopovers during autumn migration also delayed their non-breeding site arrival (0.36; [0.19; 0.52]) while there was no relation between breeding site departure timing and autumn migratory course (–0-13; [–0.34; 0.09]). Similarly, earlier non-breeding ground departures were associated with longer stopovers during the spring migration (–0.37; [–0.54; –0.19]) and longer stopovers during the spring migration with later breeding site arrival (0.34; [0.16; 0.52]; fig 5, Appendix 6 and 7).

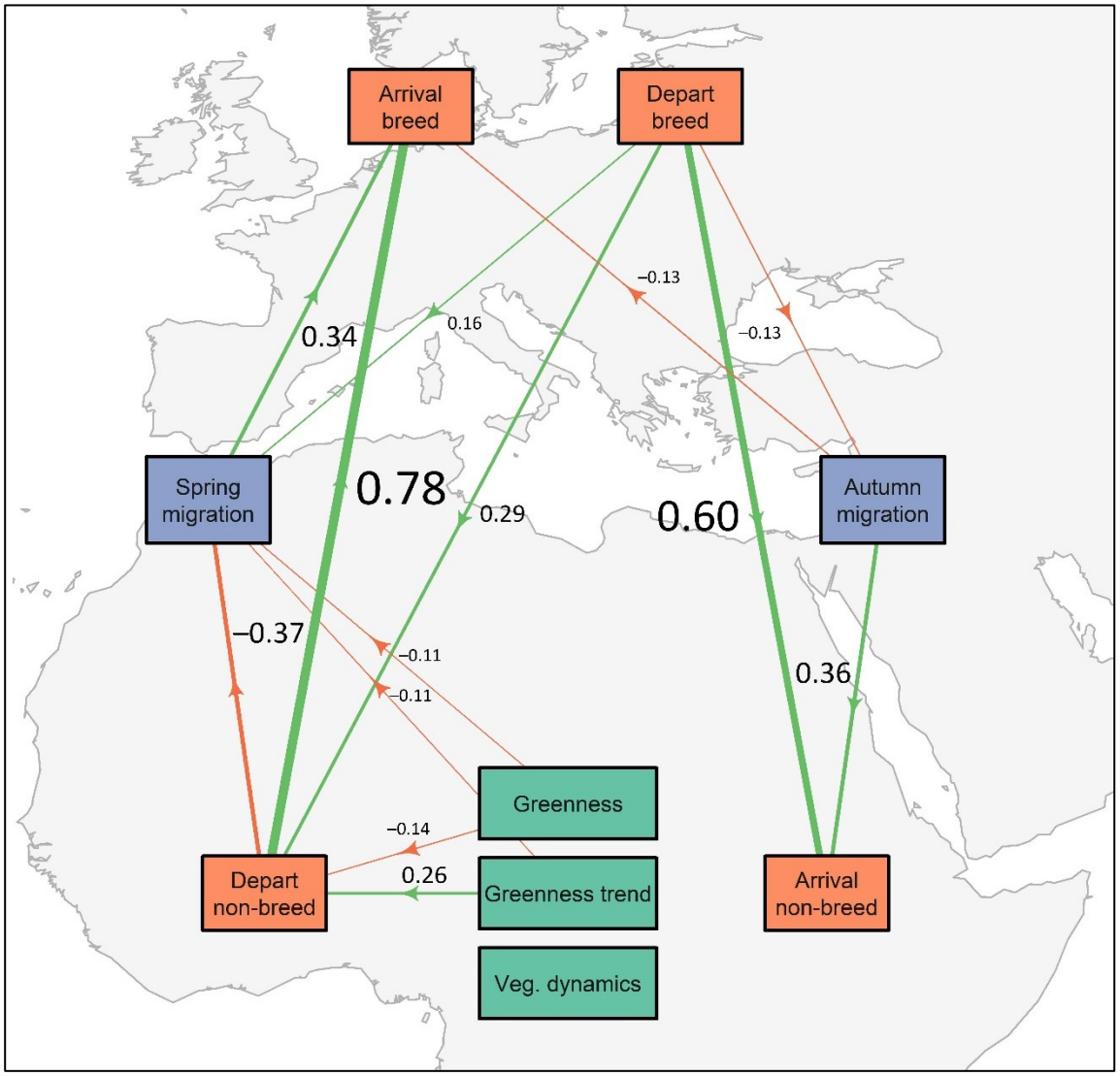

Figure 5: Result of the full annual path model describing the presence and strengths of carry-over effects between individual stages of the full annual cycle in 103 directly tracked great reed warblers. Only relationships with path coefficients over the absolute value of 0.1 are depicted. Line width corresponds to the strength of the link and colour represents direction of the relationship (green – positive, red – negative). All path coefficients with uncertainty estimates are provided in Appendix 6. The background map and location of variables represent a hypothetical situation and do not reflect the data.

We detected no paths suggesting a large or moderate relationship between the post- and pre-breeding period. Even the closest events – timing of the non-breeding site arrival and timing of the non-breeding site departure – were not related (–0.05; [–0.3; 0.22]; fig 5; Appendix 6 and 7). Interestingly, we identified a weak positive path coefficient between the timing of breeding site departure and non-breeding ground departure (0.29; [0.04; 0.54]); however, the confidence interval was very close to zero. Similarly, examination of the links between habitat conditions experienced on the non-breeding grounds and subsequent annual cycle stages revealed no large or moderate carry-over effects. However, individuals spending the non-breeding period in rapidly drying habitats slightly advanced their departure from the non-breeding grounds compared to individuals where the negative change of the habitat was not so dramatic (0.26; [0.05; 0.44]; fig 5; Appendix 6 and 7).

In general, we did not detect any statistically important differences in carry-over effects between males and females (fig 6). However, integrated greenness of the non-breeding sites tended to negatively affect the duration of stopovers (–0.17; [–0.44; 0.11]) and timing of breeding site arrivals in males (–0.26; [–0.57; 0.08]) while in females, we did not detect any tendencies for such relationships (<0.01; [–0.30; 0.35] and 0.05; [–0.33; 0.44]; fig 6; Appendix 7).

Examination of differences in carry-over effects between individuals from populations with distinct breeding latitude revealed that individuals from the southernmost breeding site (BG) tended to have on average strongest dependencies between annual cycle stages (mean of

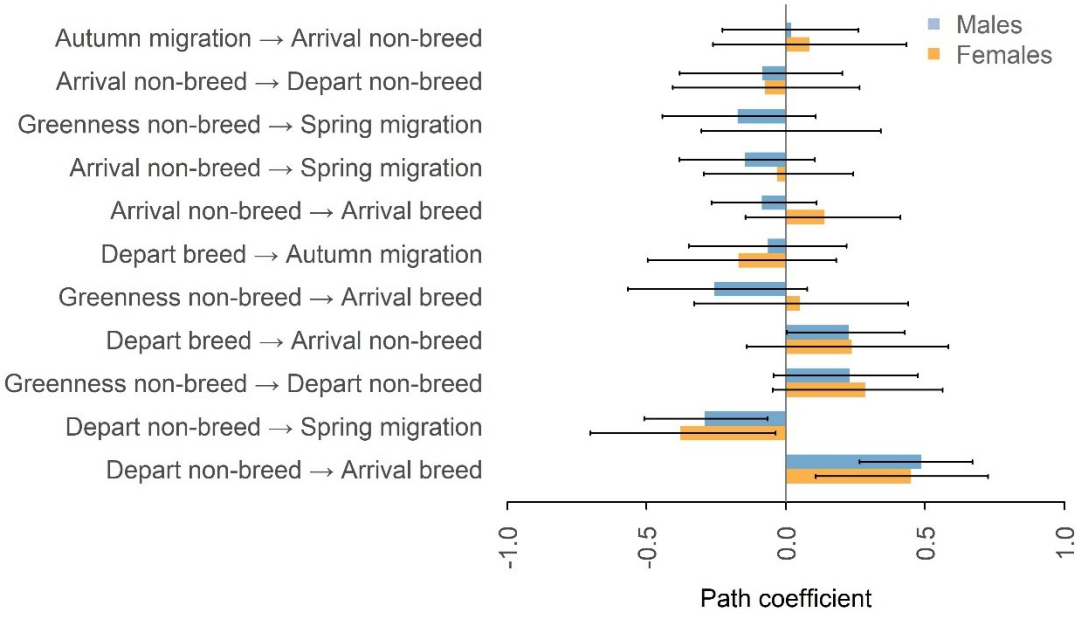

Figure 6: Sex differences in carry-over effects within the annual cycle (males = 54, females = 38). Bars are presented in descending order according to the sum of absolute path coefficients from bottom to top. Lines depict the 95% confidence intervals.

absolute path coefficient values = 0.5; 95% confidence interval = [0.26; 0.75]) compared to CZ (0.3; [0.17; 0.47]) and SE (0.3; [0.14; 0.49]). The timing of departure from the breeding sites had a positive association with non-breeding ground arrival in all populations but was very strong in BG (1.21; [0.93; 1.53]) strong in CZ (0.69; [0.38; 0.91]) and weak in SE (0.24; [<0.01; 0.46]). On the contrary, the strength of the links between the timing of events during the pre-breeding period was the opposite (fig 7). A strong relationship between timing of non-breeding departure was detected in individuals breeding in SE (0.76; [0.62; 0.87]), slightly weaker in individuals from CZ (0.67; [0.45; 0.85]) and moderate in birds from BG (0.49; [0.05; 0.93]) but none of the confidence intervals differed from each other (fig 7). During the post-breeding migration, the timing of breeding site departure was also positively linked to the duration of stopovers but in SE only (0.47; [0.14; 0.72]), whereas this relationship was negative in CZ (–0.38; [–0.61; –0.06]) and BG (–0.69; [–0.87; –0.43]). Interestingly, the integrated greenness of the habitats experienced on the non-breeding grounds had a moderate negative effect on the non-breeding departure timing in individuals from BG only (–0.52; [–0.79.; –0.17]) while the effect in CZ (0.15; [–0.20; 0.47]) and SE (0.05; [–0.30; 0.40]) was negligible (fig 7). On the contrary, higher integrated greenness appeared to be related with shorter stopover during spring migration in SE (–0.19; [–0.43; 0.05]) and CZ (–0.30; [–0.56; –0.01]) but no link was found in BG (0.12; [–0.29; 0.49]; fig 7; Appendix 7).

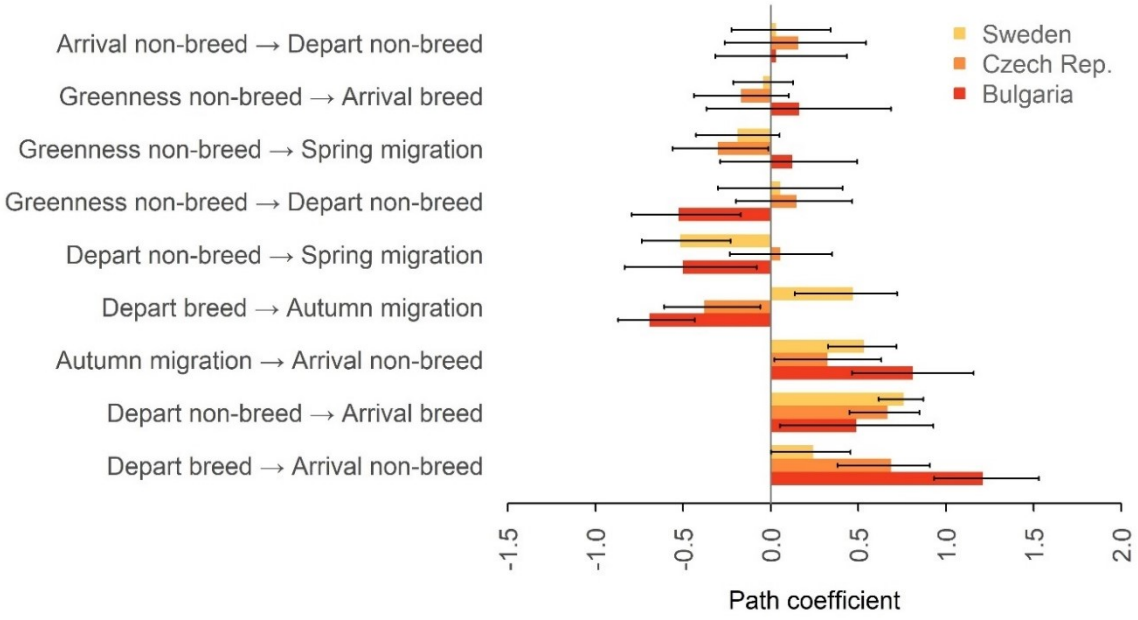

Figure 7: Carry-over effects within the annual cycle between individuals from breeding sites with different latitude (SE = 37, CZ = 35, BG = 21). Bars are presented in descending order according to the sum of absolute path coefficients from bottom to top. Lines depict the 95% confidence intervals.

Mean absolute path coefficient in the moulting period path model was 0.2 (95% confidence interval = [0.11; 0.30]) and thus very similar to 0.22 (0.09; 0.35) in the whole non-breeding period path model suggesting no overall differences in carry-over effects of the habitat conditions on the subsequent phases of the annual cycle. Moulting period path model including the stable isotopic composition of the feather samples revealed that individuals with values more depleted in ^{13}C appeared to delay their non-breeding ground departure more than individuals with more enriched values. In general, carry-over effects of integrated greenness experienced during the whole non-breeding period or moulting period on subsequent stages were almost equal (fig 8). However, stronger degradation of non-breeding habitats during the whole non-breeding period had a moderate effect on the delay of non-breeding ground departure timing (0.46; [0.20; 0.67]) and also tended to delay breeding site arrivals (–0.18; [–0.43; 0.07]). Similarly, higher vegetation dynamics experienced during the moulting period had a moderate negative effect on both duration of stopovers during the spring migration (0.45; [0.11; 0.76]) and timing of breeding site arrival (0.33; [0.12; 0.55]; fig 8; Appendix 7). Comparison of $\delta^{13}C$ values (mean = –15.74; SD = 3.25; range: [–22.31; –10.45]) incorporated into the feather tissues and integrated greenness experienced at the first non-breeding sites revealed no relationship (Pearson's ρ = 0.06; *df* = 50; P = 0.644).

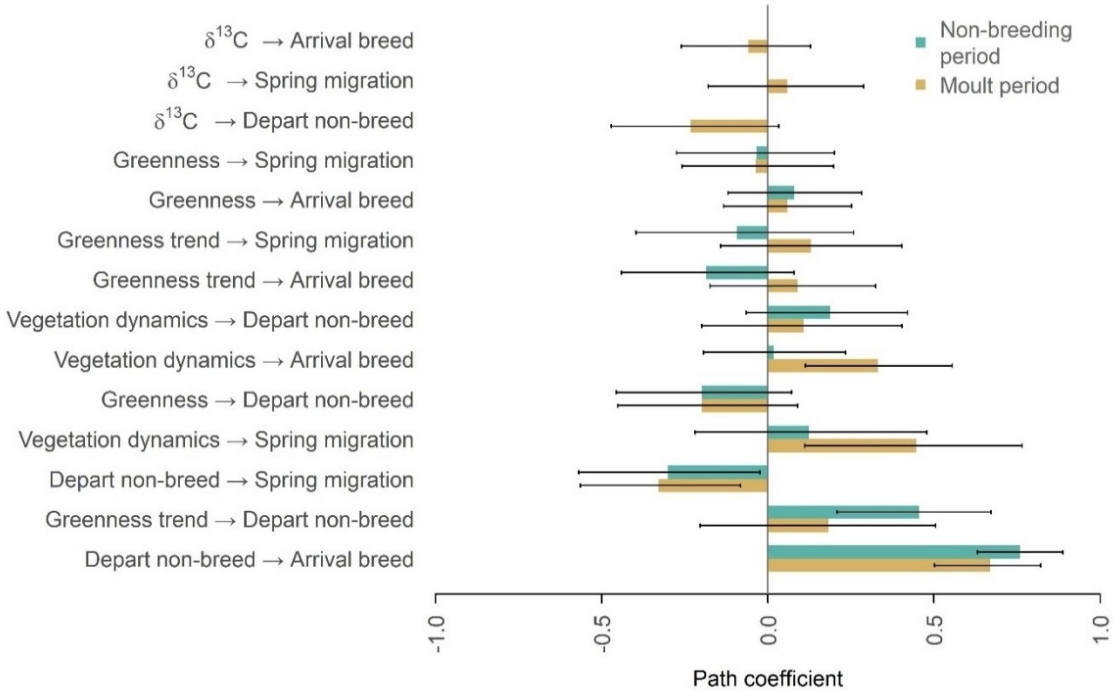

Figure 8: Carry-over effects of habitat conditions of whole non-breeding period and moulting period on the subsequent annual cycle stages (n = 52). Bars are presented in descending order according to the sum of absolute path coefficients from bottom to top. Lines depict the 95% confidence intervals.

5. Discussion

In this study, we provide unique insights into a network of dependencies between annual cycle events and non-breeding habitat conditions experienced. We supported the domino effect hypothesis as the strongest carry-over effects occurred within migratory periods only and the buffer effect of the long non-breeding period preventing accumulation of carry-over effects. Interestingly, we detected no strong effects of various environmental characteristics experienced during the non-breeding period on the subsequent annual cycle stages but vegetation drift slightly affected the non-breeding departure timing. Importantly, vegetation dynamics during the moulting period and thus the first part of the non-breeding period had moderate effect on both course of spring migration and breeding site arrival timing. Moreover, we found no clear disproportions in carry-over effects between males and females but we revealed the strongest dependencies between annual cycle events in the southernmost breeding population.

5.1. Carry-over effects within the annual cycle

Linking timing of events, movement strategies and habitat conditions experienced on the non-breeding grounds supported a domino effect which predicts the strongest relationships between consecutive events (Piersma 1987, Briedis et al. 2018, Gow et al. 2019). This pattern likely arises from a need of all individuals to follow an optimal migration strategy and time constraints of migration (Hedenström 2008). Therefore, a delay (or low habitat quality) of one event may carry over into a subsequent event and this process might be buffered with time. One of the strongest links detected was between the breeding site departure and non-breeding ground arrival and this finding is likely related to the timing and success of breeding. Individuals with advanced timing of breeding, or failed breeding attempt would have a longer period for refuelling facilitating the post-breeding migration and non-breeding ground arrival (Lindström et al. 2019). Breeding failure (Catry et al. 2013) as well as the level of parental investment (Inger et al. 2010, Bogdanova et al. 2011, Gow et al. 2019) were found to affect the timing of post-breeding migration. Parents with more offspring delay the post-breeding migration schedules more than individuals with less offspring (Inger et al. 2010, Gow et al. 2019). Similar findings were found in hoopoes (*Upupa epops*) and barn swallows (*Hirundo rustica*) where the timing of breeding completion was directly linked to the onset of post-breeding migration (Saino et al. 2017, van Wijk et al. 2017). Interestingly, Briedis et al. (2018) did not detect a link between the timing of breeding and timing of the subsequent annual cycle stages. The likely explanation could be a different schedule of complete moult in these species: while barn swallows and hoopoes change feathers on their non-breeding grounds, collared flycatchers (*Ficedula albicollis*) undertake a complete post-breeding

moult in the breeding range (Stresemann and Stresemann 1966). The moult is both time and energy demanding process (Ginn 1983, Murphy 1996) which could constrain the onset of the post-breeding migration in collared flycatchers more than in species with complete moult on non-breeding grounds.

The strongest relation in the annual cycle we found occurred between non-breeding departure and breeding site arrival. Tarka et al. (2015) found a strong selection for the early breeding arrivals in both male and female great reed warblers. Moreover, the timing of non-breeding departure seems to be largely driven endogenously (Pedersen et al. 2018) and thus high-quality individuals might both depart the non-breeding sites early and arrive at the breeding sites early. However, the early departing individuals could have a higher probability to encounter adverse weather conditions *en route* that are more likely to occur early in the season and could potentially lead to a relative delay in the breeding arrivals (Briedis et al. 2017) or could affect their survival (Lerche-Jørgensen et al. 2018). This is supported by a moderate negative effect of the non-breeding departure on stopover duration indicating that early departing individuals have longer stopovers during the spring migration but as we used a robust long-term dataset, the effect of year-specific environmental conditions on our results should be negligible.

The absence of the relationship between the post- and pre-breeding periods seems to be consistent across recent studies using full annual tracking data to detect mutual time dependencies (Briedis et al. 2018, Gow et al. 2019). Similarly, van Wijk et al. (2017) found no evidence for an impact of timing or duration of the post-breeding migration events on the timing or duration of pre-breeding events, future territory quality, or number of fledglings in hoopoes. Interestingly, Senner et al. (2014) found only a limited number of seasonal interactions between annual cycle events using the data from direct tracking of the Hudsonian godwits (*Limosa haemastica*) breeding in Alaska but their findings also support the buffer effect of the non-breeding period. Moreover, the great reed warblers could further strengthen the buffering capacity of the non-breeding period by undertaking significant intra-tropical movements as these movements were shown to improve the habitat conditions experienced during the non-breeding period (Koleček et al. 2018). However, neither collared flycatchers nor hoopoes undertake these movements (Briedis et al. 2016, van Wijk et al. 2018), and it is thus likely that the buffering capacity of the non-breeding period is not primarily related to the intra-tropical movements.

The recent findings of the most important time dependencies within the annual cycle of the long-distance migrants could be used for improving models predicting the effect of climate change on animal fitness. In general, breeding site arrivals are advancing due to an increase in average temperatures but birds often do not advance their timing as much as the climatic

conditions (Jenni and Kéry 2003, Jonzén et al. 2006, Radchuk et al. 2019). Moreover, more frequent cold spells and abnormal weather conditions have negative consequences for individuals' fitness (Briedis et al. 2017, Lerche-Jørgensen et al. 2018) and could further limit the population-wide adaptations for the climatic changes (Coumou and Rahmstorf 2012) or could act as an evolutionary trap. Therefore, incorporation of the most pronounced time dependencies between the annual cycle events could help the predictions of the future speed of adaptation or impact on the population demography.

Using a complex set of variables describing the habitat conditions during the non-breeding period, we found only a weak effect of vegetation drift on the non-breeding site departure timing. Interestingly, we detected no effect of integrated greenness or vegetation dynamics during the entire non-breeding period on any of the pre-breeding events. There are numerous studies on various species detecting the effect of non-breeding habitat conditions experienced on the timing of breeding period (e.g. Marra et al. 1998, Norris et al. 2004, Gunnarsson et al. 2005, Balbontín et al. 2009, López-Calderón et al. 2017). On the contrary, there are few studies showing only an effect of habitat conditions on the non-breeding site departure (McKinnon et al. 2015, Pedersen et al. 2016) or no effect on the subsequent phases of the annual cycle (Boone et al. 2010, Drake et al. 2014, Briedis et al. 2018). Interestingly, Sorensen et al. (2016) studying body condition of great reed warblers in south Zambia revealed a carry-over effect of the habitat conditions experienced at the moulting site (first non-breeding site) on body condition at the final non-breeding site prior to the non-breeding site departure. This relationship appeared only in one out of two years when the rainfall conditions experienced by birds in the region were low. However, none of their findings was linked to the pre-breeding period timing or breeding success of the individuals. The overall absence of the relationship between the non-breeding habitat conditions and the non-breeding departure in our study could suggest that the timing of departure is driven endogenously. This suggestion would be in accordance with studies finding a high repeatability in the event timing (Pedersen et al. 2018) and that e.g. candidate gene length polymorphism explains the variation in departure timing between individuals (Ralston et al. 2019).

There are species' life-history traits that (beside some methodological weaknesses) could explain the absence of the relationship between the non-breeding habitat conditions and timing of subsequent annual cycle stages. Firstly, great reed warblers undertake long intra-tropical movements within the African continent during the non-breeding period. These movements likely evolved to track suitable habitat conditions in highly seasonal sub-Saharan region. The amount of precipitation is higher in higher latitudes (Sultan and Janicot 2003) during the wet period but the habitat conditions quickly change during the beginning of the dry period forcing birds to move

south in search of suitable habitats (Koleček et al. 2018) with higher water availability and thus food resources. These movements would prevent great reed warblers from experiencing harsh conditions that could potentially carry over to the pre-breeding stages of the annual cycle.

Secondly, great reed warblers are medium-sized but relatively aggressive passerine species that are able to expel other species at the breeding sites after their arrival (Leisler et al. 1989). Unfortunately, there is nothing known about the interaction with other long-distance migrants or resident species on their non-breeding grounds. This hypothesis could be supported by observational studies suggesting that great reed warblers use habitats with higher water availability throughout the non-breeding period (Becquaert 1952, Ruwet 1965, De Roo and Deheegher 1969, Sorensen et al. 2015). Again, inter-specific territoriality together with intra-tropical movements could prevent the majority of individuals from experiencing conditions harsh enough that could carry over into the pre-breeding period or even to the breeding period.

Thirdly, many studies examining the link between non-breeding habitat conditions and subsequent annual cycle stages were conducted on a population level using data from multiple years (e.g. Møller 1989, Peach et al. 1991, Szép 1995, Saino et al. 2004a, Studds and Marra 2007, Wilson et al. 2011, Tøttrup et al. 2012). However, the studies where the link between non-breeding habitat conditions and subsequent annual cycle stages was studied on individual level show more equivocal results (examples above). The studies on individual level frequently use light-level geolocators to track individuals that despite a weak effect on birds (Bodey et al. 2018, Brlík et al. 2019) obtain data solely from individuals that successfully returned to the same breeding site. Similarly, other studies on individual level use only birds that survived the pre-breeding migration, successfully returned to the breeding site, managed to establish a territory and attempt to breed. Therefore, the carry-over effects of the non-breeding habitat conditions used by survived individuals could be biased compared to studies working on a population level and usually comparing multiple years of observations and survival in populations.

Finally, there are few methodological aspects that could partly explain the absence of the relationship between habitat quality at non-breeding sites and pre-breeding period events. To our knowledge, we here used the most complete approach to describe habitat quality of the non-breeding sites as we combined multiple characteristics describing overall vegetation productivity, dynamics and trend. However, NDVI data used could be biased due to the imprecision of the positions derived from the light-level geolocators. Positioning of the individuals from light-level data using a threshold method is based on the estimation of the day-/night length (Hill 1994, Lisovski and Hahn 2012) and can be sometimes imprecise or inaccurate (Lisovski et al. 2012). Therefore, position estimates could be affected by multiple factors such as habitat use, weather

conditions, topography or behaviour of the individual. Especially, habitat use might be problematic in our case as great reed warblers use dense shrub and wetland habitats that could potentially underestimate daylength resulting in the overestimation of latitudes. Moreover, potential time-asymmetric activity of the individual during dawn and dusk could affect longitude estimates as the local noon would be shifted.

As geolocator-derived positions can be imprecise, we decided to account for this error during NDVI data collection. We used a 44×44 km area of potential occurrence around each position during the period when the bird was stationary to account for the possible imprecision in the position estimate. Moreover, we *a priori* assumed that great reed warblers use more wet areas that are reflected by higher integrated greenness values due to higher water availability (fig 3) and we extracted a weekly 3rd quartile data within the area of potential occurrence. We also decided to use this approach as positions derived from the geolocators might occur outside wetlands that are frequently on a small spatial scale. However, the comparison of multiple weekly metrics used for the habitat condition assessment revealed no strong differences in carry-over effects within the annual cycle (Appendix 5B). Therefore, we conclude that the wetland habitats likely used by the great reed warblers in their non-breeding grounds are usually of very small size and thus not detectable when using a 4km resolution of NDVI data. To test for the sensitivity of our result to the imprecision of the position derived from the geolocators, we collected remotely sensed data from two larger areas of potential occurrence but found no differences (Appendix 5A). Taking into account all aspects possibly affecting the habitat condition metrics, we conclude that the data we collected should still reflect the overall habitat condition patterns.

Finally, despite a high spread of tracked individuals on their non-breeding grounds (Koleček et al. 2016, Finch et al. 2017), birds from one population visited regions usually partly separate from the region used by other populations (fig 1). This fact could affect the test of habitat quality on their non-breeding ground between individuals from different populations. Regions in the northern sub-Saharan region slightly differ in topography and vegetation structure – homogeneity of environment (Tuanmu and Jetz 2015) – that could potentially affect the NDVI data collected and thus analysis of the relationship between integrated greenness and the subsequent annual cycle phases. However, we scaled and centred data within each population and this approach should avoid impact of possible small-scale variation in habitats in the sub-Saharan region.

5.2. Carry-over effects of habitat conditions during moult period

We did not identify any differences between carry-over effects of integrated greenness during the whole non-breeding period or the moulting period on subsequent annual cycle phases; only the

$\delta^{13}C$ values from the feather samples grown at the first non-breeding sites tended to affect the timing of non-breeding ground departure. Importantly, vegetation dynamics experienced during the moulting period carried over into the spring migration and affected breeding site arrival timing; simultaneously, vegetation drift of the habitats during the whole non-breeding period affected only the timing of non-breeding ground departure. Interestingly, we did not find any correlation between integrated greenness values from the moulting period and the $\delta^{13}C$ values.

The vegetation dynamics during the moult period affected both spring migration course and breeding site arrival timing while the vegetation drift during the whole non-breeding period affected only the non-breeding departure timing. During the great reed warblers' arrival to the first non-breeding site, the vegetation conditions steadily improve in northern sub-Saharan region (fig 3). This period coincides with the end of the rain season and the vegetation conditions reach its annual maximum. However, the rest of the non-breeding period is typical of dramatic drying of the vegetation (fig 3). We thus hypothesise that the higher vegetation dynamics during the moult period could reflect the habitats where vegetation did not improve constantly due to local environmental and weather events or habitats where the vegetation senescence started early in the season. This unpredictability of the environment seems to have a stronger negative impact than the less productive habitats experienced as indicated by no evidence for a carry-over effect of the integrated greenness. On the contrary, the overall trend of the habitat conditions over the whole non-breeding period carried over to the departure timing as this variable reflects both dramatic increase and decrease during the individuals' occurrence on the non-breeding grounds. Due to the absence of studies using such a complex set of variables to describe the impact of non-breeding habitat conditions and studies considering the effects of vegetation quality and its dynamics during the moulting period, we cannot discuss our results into much detail and compare the impact on other species. However, we encourage future studies to focus on the habitat conditions and timing of the moulting period and its impact on the subsequent annual cycle phases to test our finding in other species.

There is a considerable number of studies assessing the carry-over effects of non-breeding habitat quality to the breeding period of long-distance migrants using stable isotope composition of bird tissues (Norris and Marra 2007). Many of these studies found a negative effect of low-quality habitats experienced on the non-breeding grounds on body condition during the pre-breeding period (Marra et al. 1998, Bearhop et al. 2004, Studds and Marra 2005, González-Prieto and Hobson 2013, López-Calderón et al. 2017); timing of the pre-breeding and breeding period events (Marra et al. 1998, Drake et al. 2013, López-Calderón et al. 2017) or breeding success (Norris et al. 2004, Gunnarsson et al. 2005, Reudink et al. 2009, Drake et al. 2013, Goodenough et

al. 2017, López-Calderón et al. 2017). Despite a number of studies providing evidence for the link between the stable isotopic composition of tissues and timing of subsequent events or breeding success, there are also studies that found no or almost no evidence for such relationship (Drake et al. 2014, Pedersen et al. 2016, Briedis et al. 2018). According to our results, the stable carbon ratio incorporated into feather samples tended to impact only the non-breeding departure timing. Contrary to our prediction, this suggests that the use of more mesic habitats during the moulting period would lead to delayed non-breeding site departures but the use of habitats did not carry over into the subsequent phases of the pre-breeding period. As the confidence interval of this relationship overlapped zero and did not carry over into the subsequent phases of the annual cycle, we conclude that the result might be a statistical artefact. Moreover, the wide range of isotopic values from feathers suggest that individuals used a wide variety of habitats during the feather growth. However, to fully explain the result presented, there is a need for a systematic evaluation of the stable isotopic values in different habitats, in different time periods in different regions as the current knowledge about $\delta^{13}C$ values as markers of habitat quality comes mostly from Central and South American habitats (González-Prieto and Hobson 2013).

Despite the commonly accepted notion that water availability in the habitat correlates with integrated greenness and $\delta^{13}C$ values, we found no relationship between these two variables. $\delta^{13}C$ values reflect water availability in the area through the ratio of C_3 and C_4 plants (O'Leary 1981, Farquhar et al. 1989) while integrated greenness through the amount of chlorophyll and number of leaves (Pettorelli 2013). The absence of the relationship between $\delta^{13}C$ values and integrated greenness in our study could be explained by the differences of spatial scales used. While we collected integrated greenness values from a broader area of 44×44 km, the $\delta^{13}C$ values are more likely very local and reflect habitat use on a fine spatial scale (Sorensen et al. 2015) – the area where the individual occurs during the feather keratin synthesis. As such, the $\delta^{13}C$ values were independent of the position derived from the light-level recordings that could be biased due to many factors such as weather conditions, topography, habitat or behaviour of the individual (discussed above; Fudickar et al. 2012, Lisovski et al. 2012).

There are also few methodological aspects regarding the moulting period duration, location of the moulting period and possible inter-tissue variation in stable isotopic signal that could affect our results where the stable isotopic composition was used. Firstly, inconsistency in the onset of moult could lead to differences in the location where the complete change of feathers took place. Therefore, our stable isotopic signal would reflect a different location in these individuals than we assumed and it would be thus impossible to compare the values between individuals. There are two studies that found a small proportion of adult great reed warblers

undertaking complete moult in the southern parts of the breeding range (Spina 1990, Copete et al. 1998). However, despite a very intense ringing effort in Europe, there are only individual cases of the complete moult recorded in this region. These individuals were found to suspend the moult at the site and the post-breeding complete moult is very likely not a general pattern occurring in majority of individuals breeding in Europe. On the contrary, none of the studies from sub-Saharan Africa report such cases. Similarly, some individuals could undertake a complete moult at second or third non-breeding site in Africa instead of first non-breeding site as assumed. For this case, however, there is not a single study or report of this behaviour. On the contrary, multiple studies from different sub-Saharan regions found individuals in the process of complete moult in the first part of the non-breeding period in northern parts of the non-breeding range (Hedenström et al. 1985, Bensch et al. 1991). Similarly, the individuals caught during the late part of the non-breeding period in southern parts of the non-breeding range had fresh plumage (Pearson 1975, Sorensen et al. 2016). Using a robust dataset of individuals for the analysis, we believe that our assumptions are correct and our results thus reflect the behaviour of the individuals.

The assumption of the duration of the complete moult in the great reed warbler could bias our result in a similar way as the assumption of the moulting location. The estimated duration of 77.5±24.1 days (mean±SD; n = 4; according to Hanmer 1979, Bensch et al. 1991) is in accordance with the duration of complete moult of vast majority of European passerine species with average of 65 days (Ginn 1983). The duration of complete moult in tropical resident species is slightly longer and could last from approximately 80 to 120 days (Silveira and Marini 2012, Moreno-Palacios et al. 2018) which is still very similar to the duration of moult in great reed warbler and coincides with the length of the first non-breeding period estimated from our geolocator data (87.5±21.1 days, mean±SD; n = 103). It is also possible that some of the tagged great reed warblers could have suspended the complete moult at the first non-breeding site and finished it during the later stages of the non-breeding period. However, missing feathers increase drag and thus energetic expenditure of flight (Tomotani et al. 2018) and the long intra-tropical movements (Koleček et al. 2018) would likely be very energetically demanding. Moreover, there is no evidence for such behaviour in the literature. We thus believe that the stable isotopic signal from feather samples should reflect the period when the bird occurred at the first non-breeding site.

Finally, the use of different feather types in different populations (see *Data collection*) could potentially affect our results where and when the feather synthesis occurred. However, we centred all values within the population and we should thus eliminate the potential differences in the stable isotopic signal between tissues and thus populations. Moreover, some studies focusing on the between-tissue variation in passerines found no differences (Larson et al. 2013, Bontempo

et al. 2014, Morra et al. 2018, Reese et al. 2018) or the variation in isotopic signal that did not exceed the inter-individual variation (Robillard et al. 2017). On the other hand, the variation between the feather types could be species-specific as the finding of the high between-feather type variation in black-throated blue warblers (*Setophaga caerulescens*) could suggest (Graves et al. 2018).

5.3. Sex differences in carry-over effects

We detected no differences in carry-over effects within annual cycle events between males and females. However, higher integrated greenness experienced during the non-breeding period by males tended to shorten their stopovers during the spring migration and advance breeding site arrivals. These patterns were not observed in females where the path coefficients were close to zero. Therefore, males using lower-quality habitats would have a higher probability of being delayed during the migration and on their breeding site arrival with corresponding consequences for the individual fitness (Hasselquist 1998, Tarka et al. 2015). We thus supported our prediction of stronger carry-over effects in males than in females within the pre-breeding period; however, the strongest difference occurred in carry-over effect of non-breeding habitat quality instead of timing of events.

The current knowledge on the sex-specific carry-over effects within the annual cycle is equivocal. The results found in current literature provide support for all possible combinations of effects: effect of non-breeding habitat quality on body condition and reproductive success in adult males only and missing relationships in females and young males (López-Calderón et al. 2017); stronger effect of non-breeding habitat quality in females affecting both timing of breeding and reproductive success (Saino et al. 2017); link between non-breeding habitat conditions and breeding site arrival only in males but effect on offspring fledgling date in females (Norris et al. 2004); strong habitat segregation of males and females where adult males occupy more productive habitats that enhance their condition and survival (Marra and Holmes 2001, Studds and Marra 2005), or a relation between non-breeding habitat conditions and arrival timing in young females only but its absence in old females and males (Drake et al. 2013). There is thus a need for more systematic evaluation of the possible sex-specific carry-over effects of the non-breeding habitat conditions to the subsequent annual cycle stages.

Our finding of the few differences in carry-over effects between males and females could also be explained by a limited sexual dimorphism and absence of sexual dichromatism in great reed warbler (Cramp 1992) suggesting similar fattening process and flight radius (Alerstam and Lindström 1990). Moreover, none of the previous studies of migratory behaviour of great reed warblers found any evidence for sexual segregation on the non-breeding grounds (Lemke et al.

2013, Horns et al. 2016, Koleček et al. 2016, 2018). As previously discussed, intra-tropical movements follow the habitats with better vegetation conditions and could thus prevent individuals from experiencing harsh condition that could carry over into the subsequent phases. Moreover, relatively strong inter-specific competition with African resident species might prevent individuals from occupying low quality habitats. Nevertheless, this hypothesis would need to be tested on the non-breeding grounds.

5.4. Population differences in carry-over effects

The strongest carry-over effects within the annual cycle were detected in Bulgaria while these relationships were weaker and comparable in individuals breeding in the Czech Republic and Sweden. There are multiple aspects possibly affecting the differences in these carry-over effects: (i) the species' biogeography and likely geographical diversity in migratory behaviour, (ii) differences in the distance between non-breeding and breeding sites, or (iii) differences in the geography *en route* and conditions at stopover sites.

Genetic data suggest that distribution of the great reed warbler was restricted into two main refugia during the last glacial period (Bensch and Hasselquist 1999, Hansson et al. 2008). Likely, the selection pressures on the migratory behaviour differed between these two populations at that time and could persist until the breeding range expansions to a current extent. The resulting differences could involve different non-breeding strategies such as barrier crossing, stopover duration, or loop migration. Especially, the loop migration pattern of the Bulgarian and Turkish population differs from other tracked populations (Koleček et al. 2016) and is in accordance with phylogenetic diversity between populations (Hansson et al. 2008). While Bulgarian and Turkish birds undertake the post-breeding migration directly towards their first non-breeding sites and return using more eastern route through the Middle East region (anti-clockwise loop migration), other populations show only small differences between post- and pre-breeding migratory route with predominantly clockwise loop migration (Koleček et al. 2016). Moreover, habitat heterogeneity could slightly differ between non-breeding grounds of individual populations (Tuanmu and Jetz 2015). Bulgarian and Turkish individuals spend the boreal winter in central and eastern sub-Saharan Africa and undertake extensive intra-tropical movements during the non-breeding period towards south and south-east whereas individuals breeding in Central and Western Europe use the western sub-Saharan region and undertake shorter movements within the non-breeding quarters (Koleček et al. 2018).

Especially, the differences in topography *en route* and migratory distance between populations could explain the dissimilarities in carry-over effects we found. Birds breeding in Bulgaria rarely stop over during the post-breeding migration (Koleček et al. 2016) and their post-

breeding migration thus consists mainly of the few quick flights over the Mediterranean Sea and the Sahara Desert (Adamík et al. 2016, Koleček et al. 2016). The timing of breeding site departure thus directly affects the non-breeding ground arrival compared to populations where birds stop multiple times and the duration of stopovers vary (Koleček et al. 2016). On the contrary, the strength of the carry-over effects almost did not differ between populations during the pre-breeding migration. We suggest that the absence of the predicted differences could arise from the differences in timing of the non-breeding site departure in the great reed warbler. The individuals from southernmost breeding site depart earlier than individuals from other populations (Koleček et al. 2016) and have thus a higher probability to encounter cold spell *en route* that could delay the timing of breeding site arrival (Briedis et al. 2017). The individuals from central and northern European populations depart later but have to travel larger distances, to higher latitudes that again increase probability of encountering harsh environmental conditions delaying the spring migration (Briedis et al. 2017). We thus conclude that the differences in pre-breeding timing between populations with distinct breeding latitude could diminish differences in carry-over effects.

The variability in the final non-breeding location and potentially weaker endogenous control of the timing could explain the strong carry-over effect of the non-breeding habitat conditions in the southernmost population as this carry-over effect was negligible in Czech and Swedish population. Part of the individuals breeding in Bulgaria undertake significant intra-tropical movements to southern parts of the Congo Basin while the others move within the northern sub-Saharan region only (Koleček et al. 2018). These differences in final non-breeding location could lead to differential habitat use, affect migratory distance and thus timing of pre-breeding migration. These differences could be linked to differential response of individuals to overall greenness experienced on the non-breeding grounds and could thus affect the average strength of the carry-over effect in the population we detected. Moreover, the strong relationship between the non-breeding ground quality and the timing of departure could suggest a weak endogenous control of the pre-breeding timing in this population (discussed above). As there is almost no evidence for our suggestions, we encourage future studies to focus on the impacts of the final non-breeding site location on the subsequent timing of annual cycle events, the repeatability of the event timing in repeatedly tracked individuals and the genetics driving the differences in the timing of events.

6. Conclusion

In this study, we uncovered the complex of links between full annual cycle events and non-breeding habitat conditions using a robust dataset of full annual tracking, spatiotemporally explicit remotely sensed data and stable isotopic signals from feather samples.

We supported previously proposed hypotheses of a domino effect between consecutive events and a buffering capacity of the non-breeding period. On the contrary, our results suggest only a weak effect of the habitat quality experienced during the entire non-breeding period on the subsequent annual cycle stages. The main explanation for the absence of this relationship could be the life-history of the great reed warbler. The great reed warbler is known to be a strong inter-specific competitor at the breeding sites, undertaking large intra-tropical movements to track habitat changes and using habitats with high water availability year-round. These characteristics and behavioural adaptations could help individuals to secure the most stable and productive sites even in the seasonally dynamic sub-Saharan region.

Importantly, we unveiled a moderate effect of the vegetation dynamics during the moulting period on the spring migration strategy and breeding site arrival timing. We thus unveiled a period when birds seem to be sensitive to unpredictability of the habitat change that further carry over into the timing of breeding site arrival and has a potential to affect breeding performance of the individual. We also detected strongest relationships between annual cycle events in the southernmost population compared to breeding populations from central and northern Europe but almost no differences in carry-over effect between males and females.

To conclude, future challenges in the field of carry-over effects are to test the sensitivity of species with various moulting schemes to the environmental conditions during energetically demanding moult. We also encourage to study the interaction between migratory and resident species on the non-breeding grounds and uncover the effect of competition strength of individual migratory species on the carry-over effects of non-breeding habitat quality. Specifically, competitive abilities could affect spatial segregation of sexes, age-classes or individuals in poor conditions into suboptimal habitats in some species. Finally, the number of studies focusing on the delayed fitness consequences, time dependencies within the full annual cycle or impact of habitat conditions on subsequent phases of the annual cycle is growing and these results could be summarized in a quantitative review to unveil general trends, potential differences between migratory systems and groups of species.

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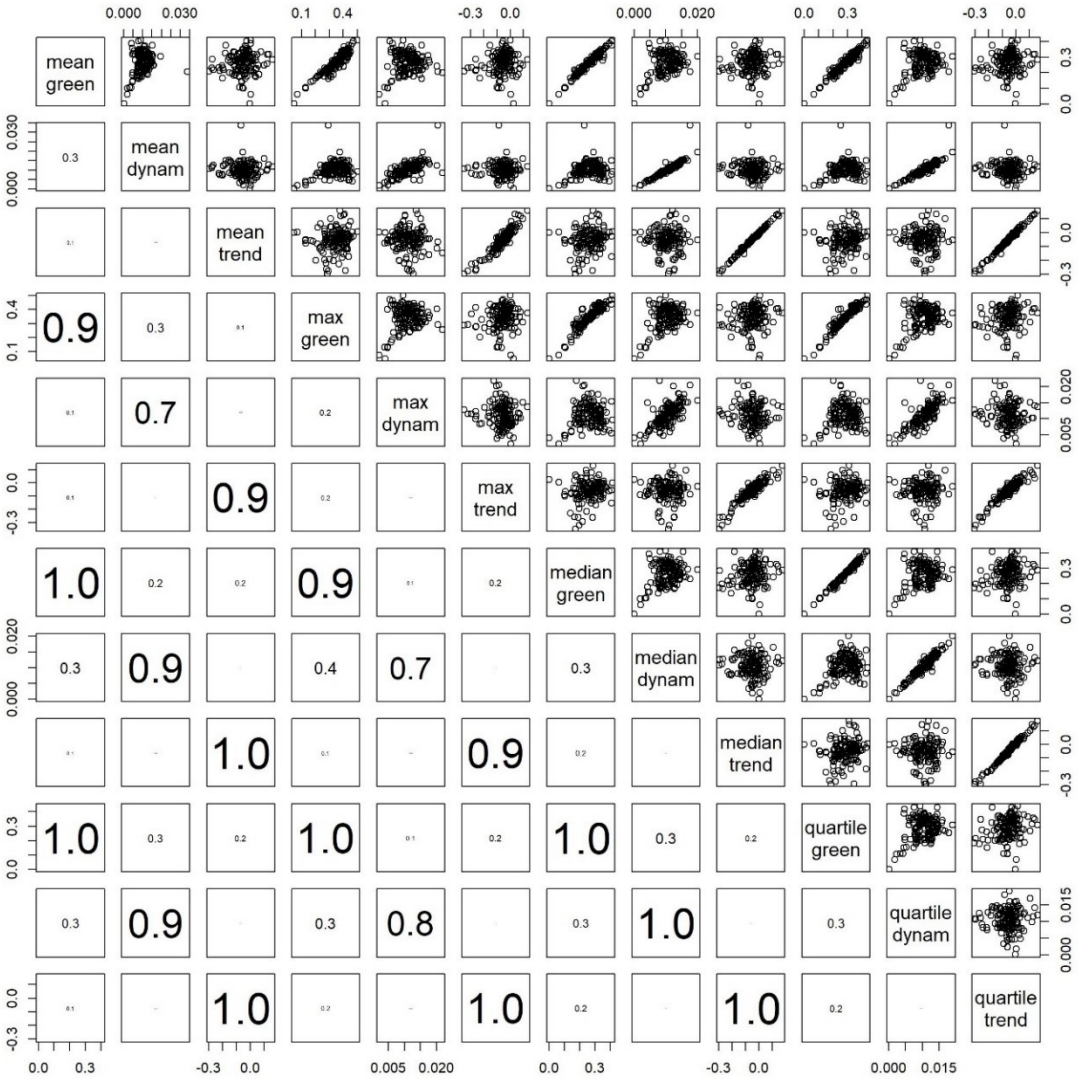
8. Appendices

Appendix 1: Number of males and females with full annual tracks recaptured in specific years and populations including information on geolocator type and its mass.

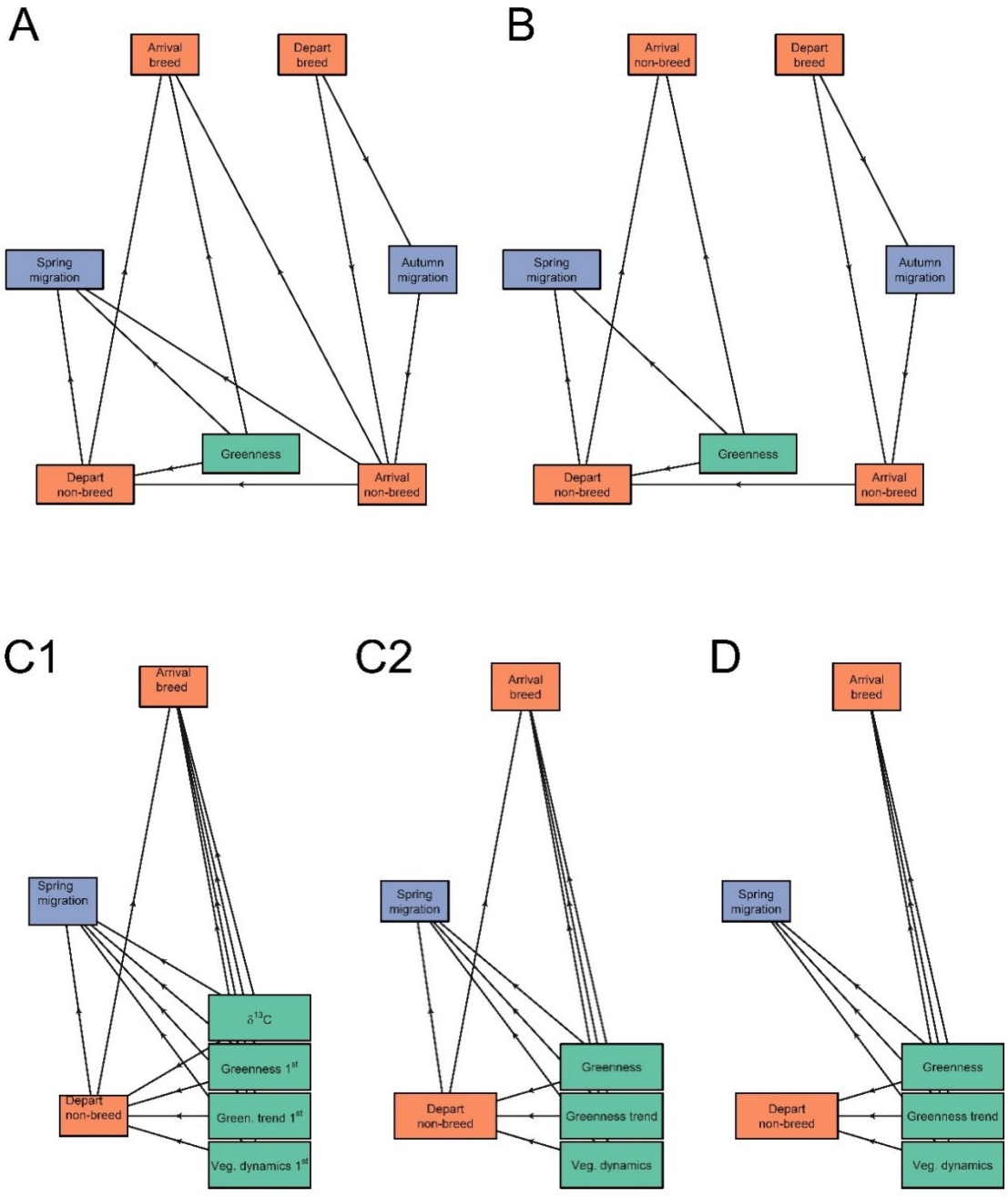
Population	Year of recapture	Males	Females	Geolocator type	Mass (g)
Sweden	2010	5	0	Mk12-SAD	1.0
	2011	2	1	Mk12-SAD	1.0
	2012	1	2	Mk20	1.0
	2013	7	1	Intigeo-P65C2J7	1.0
	2014	5	4	Intigeo-P65C2-7	1.0
	2015	0	5	Intigeo-P65C2-7	1.0
	2016	0	4	Intigeo-P65C2-7	1.0
Czech Republic	2013	3	4	SOI-GDL1	1.2
	2014	0	0	SOI-GDL1	1.2
	2015	2	1	SOI-GDL1	1.2
	2016	10	5	Intigeo-P65B1-7	0.7
	2017	4	0	SOI-GDL3 PAM	1.5
	2018	5	1	SOI-GDL3 PAM	1.5
Bulgaria	2013	2	1	SOI-GDL1	1.2
	2016	6	5	SOI-GDL3 PAM	1.5
	2017	2	5*	SOI-GDL3 PAM	1.5
Turkey	2014	4	0	Mk12-SAD, Mk20	1.0
Kazakhstan	2018	6	0	Intigeo-P65C2-7	1.0

The asterisk denotes a sample from one individual of unknown sex.

Appendix 2: Pair-wise correlations (lower panels) and scatterplots (upper panels) of different metrics used to extract the weekly value from an area of potential occurrence. Each value or plot represents a combination of either a mean, maximum (max), median, or 3rd quartile (quartile) and habitat metric – integrated greenness (green), vegetation dynamics (dynam) and greenness trend (trend) for each individual. Values in the lower panels represent the Pearson's correlation coefficients and their size corresponds to the strength of the correlation.



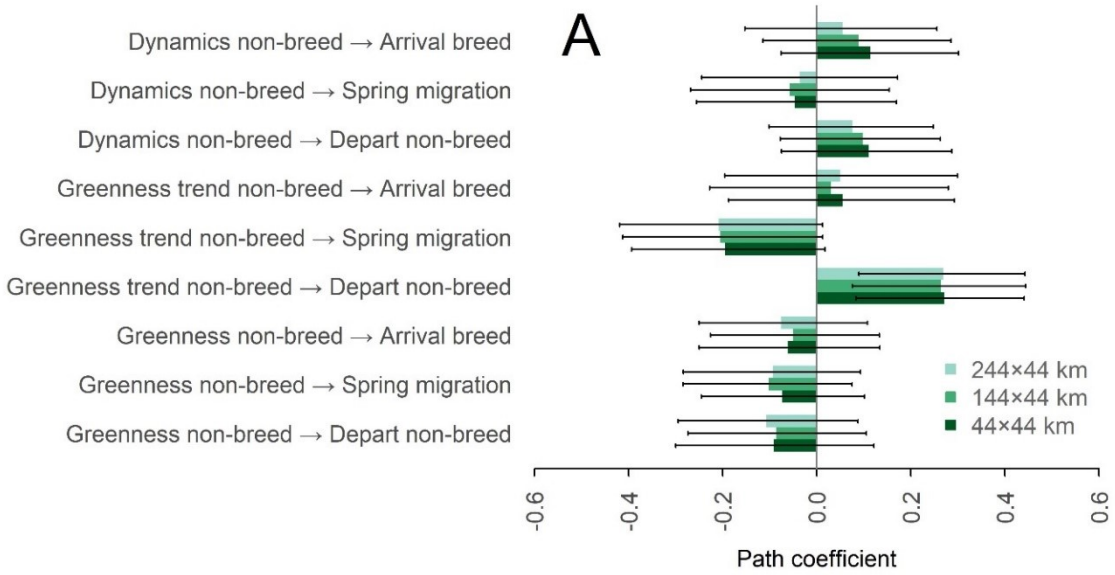
Appendix 3: Reduced path models for testing the differences in carry-over effects (A) between sexes (set of path models 2; maximum number of relationships = 3), (B) between populations breeding at different latitudes (set of path models 3; n_{max} = 2), (C1 and C2) testing differences in impacts of habitat conditions experienced during moult period (C1), or whole non-breeding period (C2) on the subsequent annual cycle stages (set of path models 4; both n_{max} = 5). For testing sensitivity of results using multiple areas of potential occurrence and multiple weekly habitat condition metrics, we used reduced path model D.

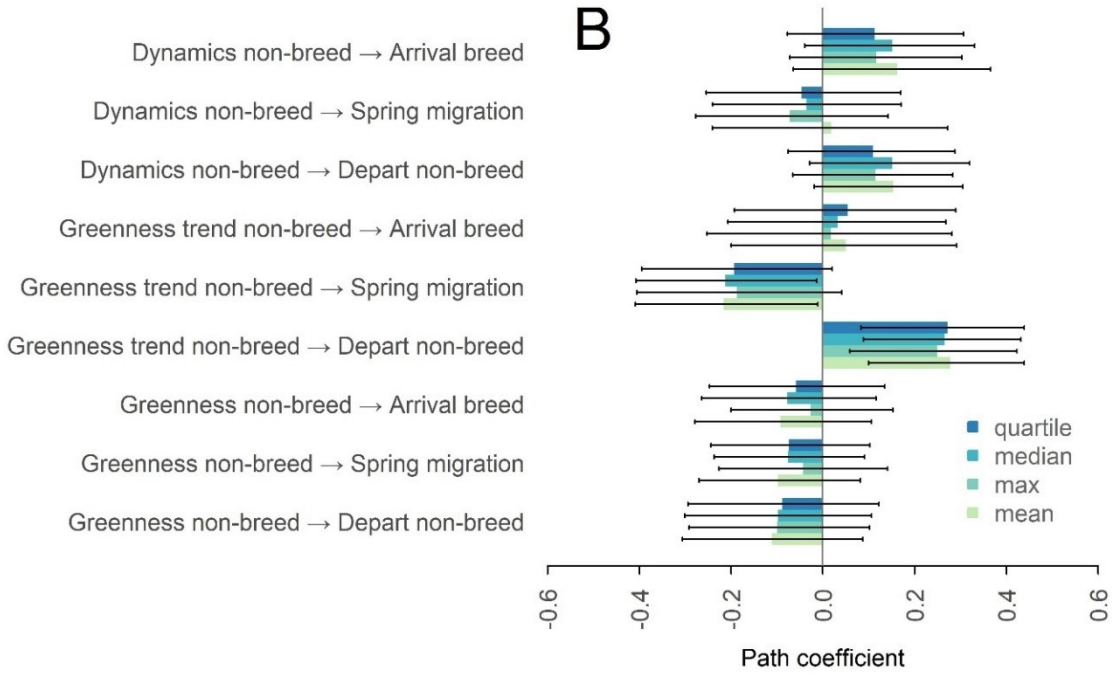


Appendix 4: Results of the linear mixed effect models testing for between-year differences.

Response variable	*F*	*P*	$R^2_{marginal}$	$R^2_{conditional}$
Departure breeding	1.50	0.170	0.09	0.29
Autumn migration	1.77	0.093	0.10	0.34
Arrival non-breeding	0.58	0.790	0.03	0.28
Departure non-breeding	0.91	0.516	0.03	0.68
Spring migration	1.83	0.082	0.12	0.39
Arrival breeding	0.18	0.993	0.01	0.30

Appendix 5: Sensitivity analyses for the area of potential occurrence (A) and weekly NDVI measures used for habitat condition assessments (B). Path coefficients are presented alongside their 95% confidence intervals.





Appendix 6: Paths considered in path model examining relationships within all stages of the annual cycle (path model 1), path coefficients (direct effects), their 95% confidence intervals and indirect path coefficients. Paths with 95% confidence interval of the direct effects not overlapping zero are in bold.

Path	*Path coefficient (direct effect)*	*95% CI*	*Path coefficient (indirect effect)*
Depart breed → Autumn migration	–0.13	(–0.34; 0.09)	0.00
Depart breed → Arrival non-breed	0.61	(0.46; 0.74)	–0.05
Depart breed → Depart non-breed	0.29	(0.04; 0.54)	–0.04
Depart breed → Spring migration	0.15	(–0.06; 0.37)	–0.14
Depart breed → Arrival breed	0.00	(–0.17; 0.18)	0.24
Autumn migration → Arrival non-breed	0.36	(0.19; 0.52)	0.00
Autumn migration → Depart Non-breed	0.11	(–0.11; 0.32)	–0.02
Autumn migration → Spring migration	–0.03	(–0.22; 0.16)	–0.06
Autumn migration → Arrival breed	–0.13	(–0.27; 0.02)	0.05
Arrival non-breed → Depart Non-breed	–0.05	(–0.3; 0.22)	0.00
Arrival non-breed → Spring migration	–0.09	(–0.32; 0.15)	0.02
Arrival non-breed → Arrival breed	0.05	(–0.2; 0.29)	–0.06
Greenness → Depart non-breed	–0.14	(–0.34; 0.07)	0.00
Greenness → Spring migration	–0.11	(–0.27; 0.06)	0.05
Greenness → Arrival breed	0.03	(–0.09; 0.16)	–0.13
Greenness trend → Depart non-breed	0.26	(0.05; 0.44)	0.00
Greenness trend → Spring migration	–0.11	(–0.3; 0.09)	–0.09
Greenness trend → Arrival breed	–0.07	(–0.27; 0.11)	0.13
Vegetation dynamics → Depart non-breed	0.09	(–0.1; 0.28)	0.00
Vegetation dynamics → Spring migration	–0.03	(–0.23; 0.17)	–0.03
Vegetation dynamics → Arrival breed	0.02	(–0.1; 0.13)	0.05
Depart non-breed → Spring migration	–0.37	(–0.54; –0.19)	0.00
Depart non-breed → Arrival breed	0.78	(0.64; 0.91)	–0.12
Spring migration → Arrival breed	0.34	(0.16; 0.52)	0.00

Appendix 7: Variation explained (%) by explanatory variables for each endogenous variable presented in path model 1 (PM1) and each set of path models (SPM2, SPM3 and SPM4).

Endogenous variable	*PM1*	*SPM2*		*SPM3*			*SPM4*	
		Males	*Females*	*SE*	*CZ*	*SE*	*Moult*	*Non-breed*
Autumn migration	1.6	0.4	3.1	22.4	15.1	47.7	–	–
Arrival non-breed	43.9	5.2	5.0	44.2	41.9	75.9	–	–
Depart non-breed	15.3	4.6	8.1	0.5	5.0	27.6	12.6	24.1
Spring migration	17.9	17.3	14.5	31.9	9.0	33.8	26.7	13.3
Arrival breed	54.5	29.6	23.4	56.7	43.9	18.0	54.8	48.2